THE INTERRELATIONS OF HABITAT, GROWTH RATE, AND ASSOCIATED VEGETATION IN THE ASPEN COMMUNITY OF MINNESOTA AND WISCONSIN[1]

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INTRODUCTION

Differences in habitat, even within distances of a few feet, in what seems to be a uniform environment, are characteristic of the natural conditions under which plants grow. The significance of such differences in plant occurrence and growth is as yet largely a matter of conjecture. The measurement of the growth of trees and stands and the identification and enumeration of plant indicators and plant communities are relatively simple, and comparatively satisfactory methods of evaluating them have been developed. But trees and plants are influenced in occurrence and growth by all the factors of their immediate environment. Could these be equally well evaluated, they would provide an integrated measure of habitat and a possible means for quantitative comparison. How this may be accomplished for the aspen community is considered here. The problem is to correlate certain measures of growth with the occurrence of plants associated with the aspen, and thereby to achieve a quantitative measure for the evaluation of the differences between given aspen habitats and their relative productivity. Conversely it will be possible to test the usefulness of habitat features as a means of predicting growth rate of aspen.

The complexity of any plant habitat needs no proof. It is only necessary to enumerate some of the multitude of factors involved, such as illumination and radiation, precipitation, atmospheric humidity, evaporation, air and soil temperatures, moisture, soil texture and structure, and chemical and biological complexes. The host of microorganisms in the upper layers of the soil—many of them chemists of high attainments whose activities vary greatly diurnally and seasonally—contribute to make the soil an inextricably complex and ever-changing feature of every plant habitat. At times, and where one of the factors may become critical in the continued existence of the plants, its significance may be interpreted by means of instrumental and laboratory determinations. Much the commoner circumstance, however, and the one which nearly always obtains in the aspen community, is an intermingling of all these factors in which no one is limiting. Here the combination and interpretation in terms of a scale of habitat productivity for the growth of plants must be attempted by some other means.

Such a problem might be attacked from several different angles. Samples of the different aspen habitats could be collected and analyzed to determine the physical, chemical, and biological properties of the soils. The climatic

environment could be measured instrumentally and the growth of aspen phytometers recorded for these same combinations of factors both in the laboratory and in the field. Similar records for artificial habitats in which the factors of the environment would be controlled might be attempted. These methods are, however, time-consuming and there is always a question of how accurately the conclusions can be applied to the numerous natural habitats which have not been sampled and in which the combinations of factors are different and more or less unknown. Sufficient representative permanent quadrats on which records of growth, vegetation, and environmental factors could be made periodically would serve the purpose admirably; but these would be prohibitive in number—no less than in range of distribution and period of record required.

Another method may be called the biometric, in which samples of the different aspen communities and their habitats are taken and described in quantitative and qualitative terms such that the material may be classified in numerical or other categories and conclusions drawn by biometric analysis, due regard being given to the variations exhibited and the consequent degree of reliability that may be assumed for the biometric measures. This method has the advantage that a large number and wide variety of aspen communities may be sampled in a relatively short time and, if the sample areas cover the range of variation adequately, the conclusions, within determined limits of accuracy, may be applied with some confidence to the whole aspen community in the region. This method was adopted in the present study.

COLLECTION AND COMPILATION OF DATA

The essential features of the aspen community have been described elsewhere (Kittredge and Gevorkiantz 1929), but may be here briefly summarized. The aspen community is considered to include only stands in which *Populus tremuloides* Michx. predominates. A very large proportion of the aspen stands in Minnesota and Wisconsin have originated as suckers or offshoots from the roots of a previous stand which was destroyed by fire. The new generation starts promptly and densely from the old established root system. The growth is rapid even in the first year and enables the aspen to take and maintain throughout its 40 to 70 years of vigorous development a dominant position with respect to other vegetation. Thus the trees in any given community are almost all within two or three years of the same age and

have only a minor proportion of other tree species in association with them in the dominant canopy.

The aspen community occurs abundantly and under a wide variety of conditions throughout northern Minnesota and Wisconsin. It is, however, rarely found, if at all, on dry sandy outwash formations and the less favorable peat deposits. It commonly occurs on all the other geological formations from sandy moraine to lake-bed clay, and on a large majority of the soil types of the region. This universality of occurrence makes the aspen a most advantageous community to use as a measure of different habitats.

METHODS OF COLLECTION

The field data were collected largely in 1925 and 1926 under a detailed plan designed for a somewhat more comprehensive forestry project. The pertinent portions of the plan are included in the following paragraphs. Two of the objectives of the project were: (1) To determine the possibilities for the conversion of the aspen type to one of more valuable species such as white pine, white spruce, black spruce, Norway pine, or balsam fir; and (2) to prepare tables for the aspen type to give some idea of its growth and yield and to serve as an index of site for the better soils of the region.

Temporary sample plots were selected to represent areas on which conifers had become established or were coming in under stands of aspen, and also well-stocked stands comprising as far as possible the range of site classes for aspen in the region. The plots or sample areas were one or more chains square, most of them being squares of 0.1 acre. The areas were laid out on the ground with a steel tape and compass, and so located as to represent uniform conditions of vegetation and habitat within the boundaries insofar as that was possible. The selection was limited to areas in which aspen 15 years old or older predominated among the tree species.

Measurements included diameters of all trees more than 0.5 inch d.b.h.[1] and heights of a sufficient number of trees for the construction of a curve of height on diameter for the range of diameters on each plot. Wherever possible, a few heights were also measured in stands of different densities at the same age and on the same site, to determine the effect of density on the site index. Diameters were measured with a diameter tape and heights with a Forest Service or Klaussner hypsometer. Ages were determined with an increment borer from not less than three borings in trees of approximately average diameter at heights of 1 foot above the ground or at 4.5 feet where butt rot occurred.

Where conifers less than 0.5 inches in diameter were present they were recorded by numbers of each species on a quarter-chain strip (16.5 feet wide) through the center of the plot. The ages of conifers of different sizes and species were determined by cutting or boring.

[1] D.b.h. = diameter at breast height, or at 4.5 feet from the ground.

Crown density of the overstory was estimated in tenths of total area. Shrubby and herbaceous vegetation was estimated on a similar scale based on area covered by all species combined and by the important individual species. Other species which constituted an unimportant part of the total were noted.

Soil notes included thickness of litter and humus, and texture, color, and thickness of each distinct horizon of mineral soil to a depth of 3 feet. Soil texture was determined by the appearance and feel of a sample. Topography, slope and aspect, and surface geological formation were also noted; in Minnesota the geological notes were checked by Leverett and Sardeson's maps (1915, 1917). Finally, notes were made as to the probable origin and history of each sample area, and as to any evidence of the subsequent occurrence of fire or other disturbing agencies.

If the data had been collected specifically for the kind of analysis attempted in the following pages, the methods would have been amplified or intensified in several respects. For example, the vegetation might have been evaluated more exactly by quadrat enumeration and more completely to include infrequent or inconspicuous species; soil notes might have included structural features of the different horizons and field determinations of acidity and lime, making possible in some instances more exact assignment of soils to the right soil types; and field work might have been made more uniform by the use of a single crew. However, it has appeared as the analysis has proceeded that the field data, with the exception of that from occasional plots which were obviously incomplete in some respect, are surprisingly satisfactory considering the manner and purpose of their collection.

An unforeseen difficulty, which is inherent in the natural distribution of the aspen community, is the fact that desirable sample areas from the point of view of the vegetation are disproportionately likely to be found on the narrow transitional strip between upland and swamp. This strip, being also transitional between two soil groups or types, is therefore difficult to assign to either one of them with confidence. Plants from both the adjacent habitats tend to intermingle in such situations with resulting confusion of indicator significance. In the early part of the work no attempt was made to avoid these areas.

As the field work progressed, a cumulative record was made of the number of plots obtained in different age and site-index classes. Toward the end special effort was devoted to finding and sampling communities belonging to the classes least well or not at all represented up to that time. This provided at least a moderate number of sample areas in each of the classification categories used, although it probably destroyed the value of the data as representative of any actual proportional distribution of the aspen community among the different habitats in the region.

QUANTITY AND DISTRIBUTION OF DATA

A total of 277 sample plots were available for analysis, of which for most of the particular phases of the analysis only a few were unusable because of gaps in the data recorded. They represent a range of density in aspen stands from heavily overstocked to decidedly understocked. Ages from 16 to 75 years are well represented, and there is one sample each of ages 85 and 95. Site-index values are well distributed from 41 to 82. The nine principal geological surface formations are all represented and each of them may be subdivided, with the exception of the peat, into the red or Early Wisconsin and the gray or Late Wisconsin epochs. Eight soil-texture classes had a sufficient number of samples to permit the distinction of red and gray drift areas in each of them. Fifty-four soil types are represented, although several of them by only one or two plots. The material is not sufficient for an analysis of all the individual soil types, but when the soils are condensed into 22 profile groups a reasonable number of plots are available for most of the groups, and when these plots are assigned to the 16 plant-indicator groups a sufficient number fall into each for moderately satisfactory treatment.

The fact that the material can be classified satisfactorily in these several independent ways, seems to indicate that most of the major variations of the aspen community and of its environment in the region are represented by at least a few sample plots. The actual number of plots which fall in each of the categories of these various classifications will appear in the graphs and tables in which the interrelationhips are analyzed.

In addition to the categories already mentioned, geographic distribution has some significance. The map, figure 1, shows the approximate location of the plots. Although by no means uniformly spaced, their distribution suggests that the chief variations due to geographic location within the territory under consideration have been sampled.

RELIABILITY OF DATA

That the data are probably not numerically representative of the relative occurrence of the aspen community in the different age and site-index classes in the region, has been explained as due to the special effort to find samples of the less frequent classes. It would certainly be unsafe to conclude that, because 20 percent of the plots have site indices lower than 55, the same proportion of the aspen community in the region is on correspondingly poor sites. Similarly, a statement that 20 percent of the aspen in the region is over 57 years old, as it is in the plots, would certainly be a gross exaggeration.

The relation between age and habitat distributions is probably somewhat biased also for a biological reason. No samples could be found of the older age classes on the less favorable habitats—those of site index lower than 55. This coincides with the observation that aspen dies on the poorer sites before
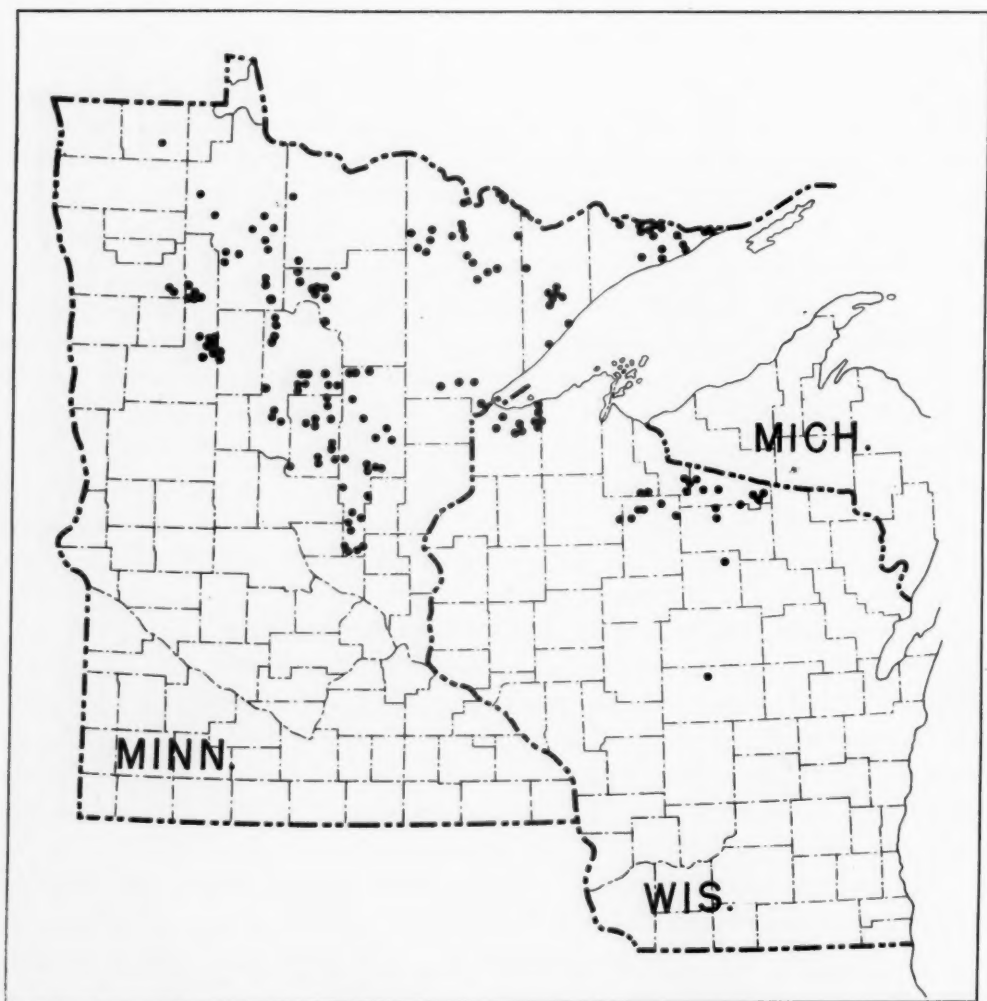
FIG. 1. Location of aspen plots in Minnesota and Wisconsin.

it reaches ages of 50 or 60 years, whereas it commonly attains ages of 75 years or more on the better sites. Whether this is due to lowered resistance to the prevalent fungus disease caused by *Fomes igniarius* (L.) Gillett, or to reduced vigor and inability to function physiologically under adverse habitat conditions, has not been determined (Schmitz and Jackson 1927). Fortunately, this bias has little significance in a study where age is not one of the variables used. It probably does affect to a slight degree the trends of the upper portions of the curves of dominant height over age and volume over age, from which the site-index and volume-index classifications were derived. Even so, the resultant earlier flattening of these curves would not affect appreciably the assignment of plots to site-index or volume-index classes. It would only tend to reduce slightly the range of these two variables at the upper ends of their distribution.

The present material, from whatever angle analyzed, shows that variations between individual measurements or plots are inherent in this as in all biological populations, no matter how homogeneous they may be. This is true of the heights of the dominant trees measured and averaged to obtain the site-index figure for a plot. It is true of the site indices of different plots in what is supposedly a uniform soil type or soil or vegetation group, and it is true of the frequency of occurrence of plant species in what appears to be a uniform habitat group. Biometric analysis enables the evaluation of the significance of means or other measures which may be derived from this variable material and used as the basis for conclusions. Two examples will make this clearer.

Soil profile groups 14 and 19 (to be shown later in figure 15) each contain five plots, the former with site indices from 59 to 66, and the latter from 65 to 78. Comparisons of the means and standard errors are given in table 1.

TABLE 1. MEANS AND STANDARD ERRORS OF SOIL PROFILE GROUPS 14 AND 19.

Item	Group 14	Group 19
Mean site index (MI).................................	62.8	71.0
Standard error of mean (σMI).......................	± 1.15	± 2.7
Standard error, percent.................................	± 1.8	± 3.8
Twice standard error of mean...........................	± 2.3	± 5.4
Twice standard error, percent..........................	± 3.6	± 7.6

The standard errors were computed by Fisher's (1930) formula,

$$\sigma MI = \frac{\sigma_I}{\sqrt{n-1}}$$

When the probabilities are adjusted by means of "Student's" (1925) tables of the probability integral of his "t" function to allow for the small number of cases, the foregoing figures may be interpreted in several ways. First, with standard errors of 1.15 and 2.7 the chances are 62 in 100 that the true mean of soil-profile group 14 lies between 61.7 and 63.9, and of group 19, between 68.3 and 73.7. The chances are the same that the true mean site index of group 14 is not in error by more than 1.8 percent and of group 19 by more than 3.8 percent. Or, if twice the standard error is used as the criterion, the chances are 88 in 100 that the true mean site index for group 14 lies between 60.5 and 65.1 and of 19, between 65.6 and 76.4, corresponding to a percentage error not exceeding 7.6. This 7.6 may be compared with the 3.6 for group 14, indicating that the latter as an average is decidedly more reliable than the former simply because the variations in the site indices of the individual plots have a narrower range, although their number is the same.

All the means and other biometric measures used in the following pages are subject to varying degrees of reliability in the same way, but these variations are taken into account in the methods themselves, not only for single measures but in comparing the differences between overlapping series of values. Twice the standard error in the normal distribution, corresponding

to a probability of 0.05, is a satisfactory limit used by most workers in deciding whether a computed measure may or may not be due to chance. The use of this criterion will appear frequently in the subsequent analyses of various groupings.

METHODS OF COMPILATION

The average height of the dominant and codominant trees of each plot was computed from the field notes and the corresponding site index obtained. Average ages were derived from the borings of sample trees. Number of trees per acre was used as a measure of density or stocking, and the volumes of the stems of the trees on a per-acre basis were computed by the use of volume tables (Kittredge and Gevorkiantz 1929). The soil categories were checked by the use of geological or soil survey maps insofar as possible. Plant identifications were checked wherever specimens had been collected. These computed values, the soil categories, and the species of vegetation for each plot were then transferred to cards to facilitate sorting into the several categories of which relationships were to be analyzed.

After a sorting of all plots into the groups to be studied, the values of individual plots in each group were plotted on dot diagrams so that the variation within each group and the relations between groups could be roughly evaluated by observation. Plots which had extreme and therefore possibly erroneous values in any group were then rechecked as to these values.

No values were discarded simply as extreme. Differences in numbers of plots basing different analyses are due rather to such omission or inadequacy of certain items of record in the field notes that the plots could not be used satisfactorily in certain specific classifications.

For parts of the plant indicator analysis a separate set of card records was set up, one card for each plant species found in the aspen community. On these cards were entered the data as to the number of occurrences of each species in other communities than aspen and on different soil types. This permitted groupings of species independent of their associations in any particular aspen plot. The records of occurrence of species in communities other than aspen were taken in part from field work by the writer in 1930, in part from published records by Cooper (1913), Gates (1912), Bergman (1923), Stallard (1929), Livingston (1905), Ruthven (1906), and Grant,[2] and in part from vegetation lists from different forest types taken by Gevorkiantz and other members of the Lake States Forest Experiment Station. Although this material was not all homogeneous or entirely satisfactory, it did in the aggregate provide a definite and reasonably reliable means of grouping the species found in the aspen community according to their most common occurrence in some other natural community.

Biometric methods have been used as tools for the testing of hypotheses

[2] Grant, M. L. The burn succession in Itasca County, Minnesota. 63 pp. [Master's thesis, Minn. Univ. Multigraphed.]

or for the determination of degree of relationship, the homogeneity of group-
ings, or the significance of differences. They do not in any sense replace the
logic of biological relationships, nor do they in themselves provide interpreta-
tion of results. They facilitate such interpretation by giving a quantitative
basis for it. The soils and plant indicators are at present expressible only in
categorical terms, and analysis of such data has required the use of methods
like those of the correlation ratio and the contingency coefficient. These
methods have been fully described and tested in the literature of biometry
and statistics. The early stages of the work were discussed in conferences
with the late Dr. J. Arthur Harris. Considerable use has been made of the
adaptations of method and tables for the application of biometric measures to
small numbers of cases by Fisher (1930).

THE REGION

The geographic location and boundaries of the region from which the data
came may be seen from the map, figure 1. Roughly, it lies in northern Min-
nesota and adjacent Wisconsin east and north of Marshall, Wadena, and
Benton counties in Minnesota and north of Rusk, Taylor, and Langlade
counties in Wisconsin.

CLIMATE

The climate of this section is, in the main, uniform. The mean annual
precipitation ranges from 23 inches at the western edge to 40 inches in north-
western Wisconsin. For the most part it is between 30 and 35 inches, of
which 20 to 25 inches falls in the growing season between April 1 and Sep-
tember 30. The snowfall is heavier and of longer duration adjacent to and
north of Lake Superior, where it may exceed 100 inches, as compared with 45
inches in the western part. The mean annual temperature at International
Falls is 35° F. compared with 41° at Milaca, Minn. Maxima of 90 to 100° F.
occur in most summers. The growing season or period between first and last
killing frosts varies from slightly less than 100 to more than 125 days a year,
although frosts may occur occasionally in any of the summer months. The
boundary between the Transition and Canadian zones, as defined by Merriam
(1894) by a mean daily summer temperature summation of 10,000° F. and a
mean for the 6 weeks (June 23 through August 7) of 64.4°, passes across
the southern portion of the section. The precipitation-evaporation ratio of
Transeau (1905), as computed for individual stations by Livingston and
Shreve (1921) at Duluth, is 1.30; and at stations not far outside the region
is as follows: Pembina, N. Dak., 0.92; Moorhead, 0.95; St. Paul, 1:02; and
Marquette, Mich., 1.33. The range within the region is probably between 1.05
and 1.40. On the whole, the differences between different parts of the region
are not of such magnitude as to cause variations in tree growth, vegetation, or
soils greater than might be found in closely adjacent habitats of contrasting
local environments.

GEOLOGY

Only the essentials of geological history as they influence the local habitats on which sample plots were taken will be outlined. In northeastern Minnesota in a belt south of the Canadian boundary—in places as much as 50 miles wide—the granites, gneisses, and schists of the Huronian and Laurentian periods outcrop freely and are little or not at all covered by glacial deposits. Elsewhere in the region the plot locations were on the unconsolidated Pleistocene deposits, which vary from a few to more than 200 feet in thickness. The earlier Kansan drift is covered by that of more recent age except in unimportant exposures along the larger stream valleys.

The Early Wisconsin glacial invasion came from the area of igneous rocks to the northeast and completely covered the region with a mantle of drift, except as the rock was scoured and left bare in northeastern Minnesota. This deposit is known as the red drift by reason of its color and is characteristically rather stony, low in lime content, and acid in reaction. Two lobes of this advance of the ice occurred in the region, the Patrician in east central Minnesota, and the Chippewa in west central Wisconsin. The more or less intermittent retreat of this ice sheet and the waters from its melting account for the variety of glacial surface formations of the eastern part of the region.

In Western Minnesota, a later invasion of ice, known as the Late Wisconsin or gray drift, advanced from or across the sedimentary formations including limestone to the northwest of Minnesota. This ice partly covered the earlier deposits with a layer of less stony drift having a relatively high lime content and less acid reaction. Postglacial stream cutting, deposition of alluvial material, and accumulation of peat have taken place since the retreat of the ice. Two large lakes persisted for many years in front of the receding ice dam. One, known as Lake Agassiz, covered a large area north of Red Lake and east into St. Louis County, and the other, Lake Duluth, occupied the western part of the Superior basin and covered a narrow strip along the north shore and a wider strip extending into Carlton County, Minn., and along the south shore in Douglas, Bayfield, and Ashland Counties, Wis. Two other lakes of considerable size in Minnesota were drained by the cutting through of land barriers—Lake Aitkin along the Mississippi River in Aitkin County and Lake Upham in Western St. Louis County. Recent botanical evidence indicates that the large sandy area in northwestern Wisconsin, formerly considered to be an outwash plain, may have been, at least in part, a shallow lake (Fassett 1929). The deposits of all of these lake beds are different from those of the surrounding higher lands.

The marked differences in the character of the glacial and fluvio-glacial deposits are due to the differences in action and interaction of the ice, its load, and the water from its melting. Deposits laid down under the ice as ground or overridden moraines, or till plains, have a large proportion of fine material, whereas the drift pushed up or laid down at the edge of the ice and more or

less sorted by water contains coarse sandy and gravelly material characteristic of the sandy moraines. In some places, shallow sheets of water deposited outwash aprons and plains, and in other places, terraces along the swollen streams. Wind had a part in the deposition of some of the sands. Other deposits were laid down in lakes as lake bed formations. Or the presence of lakes caused a sorting of the drift by the waves and the formation of lake beaches. Some of the lakes have been filled in to form peat swamps. Briefly, this is the origin of the surface geological formations which will be used as a basis of classification in a subsequent section.

These same agencies are responsible for the confusing array of hills, ridges, plains, valleys, depressions, swamps, and lakes which characterize the topography of the region. For the most part the slopes are short and gentle or hardly noticeable. In places the sandy moraines are quite hilly and the northeastern rock-outcrop section has numerous short, steep, rocky slopes. The topography is not such, however, as to cause noticeable differences in the tree growth or vegetation because of aspect or exposure. The absolute elevations vary from 602 feet at the surface of Lake Superior to slightly over 2,000 feet on some of the higher hills. This difference also is not sufficient to cause evident distinctions in vegetation or soil. The drainage, to Hudson Bay, to the Gulf of St. Lawrence, and to the Gulf of Mexico, is still immature, as evidenced by the numerous lakes and swamps and the shallowness of most of the stream valleys. This lack of adequate drainage in many areas of varying size is important in its influence on soils, plants, and trees. More complete accounts of the geology and physiography may be found in the work of Leverett (1915) and Leverett and Sardeson (1917).

Soils

The differences in geological origin of the surface formations are still apparent in the soils of the region, although in time, as the soils mature, these effects will be obscured. Actually, the classification of the soils of the region by the United States Bureau of Soils and the States in cooperation has been largely based on geological origin.[3] The soils of the aspen community were classified according to the soil types described in the Soil Survey reports wherever possible.

[3] By this system soils derived from one source, such as granite or sandstone, or under the influence of one agency, such as alluviation or weathering in situ, or having a certain content of organic matter, such as muck or peat, are classified in a major group called a series. Each series is subdivided, according to the texture or proportion of particles of different sizes, into classes. A single class of any series is called a soil type, which is the unit of classification used in the soil surveys.

More recently, under the influence of the Russian school of soil science, made available in English by Marbut's translation (1927) of Glinka's work, the tendency has been to consider the soil as separate and distinct from the geological formation with which it may be associated. This is indicated by the following definition: "The soil or solum consists of the outer unconsolidated layer of the earth's crust, from a film to several feet in thickness, which differs from the material beneath it in color, structure, texture, physical constitution, chemical composition, biological characteristics, chemical processes, in reaction and in morphology." And again, "the parent material is that from which the soil is derived by outside forces." Many of the characteristics which distinguish different soils one from another may be observed in a soil profile, a vertical section from the surface to the underlying unweathered material. The profile has several layers or horizons parallel to the soil surface which are more or less well-defined in one or more soil properties or characteristics. As a result of the development of these conceptions, the soil type has been redefined as a group of soils uniform in texture of the surface layer of mineral soil, and of uniform profile.

The aspen community was sampled on 54 different soil types. It probably occurs on almost as many more types which did not happen to be represented by any of the plots. Almost all of these types belong to the large regional group of soils of the podsolic soil province, which extends eastward from northern Minnesota and Wisconsin across Michigan and parts of Indiana and Ohio to New York and Maine. These podsolic soils have all developed under the influence of a climate and vegetation of temperate latitude. They have certain characteristics in common. The upper or A horizon has a high content of silica. The iron and aluminum constituents have in part been removed and have accumulated in the underlying B horizon. Some of the iron from the A horizon has been entirely lost in the drainage water. The alkali and alkaline earth compounds have been lost in large part from both A and B horizons. A part of the soil types are true podsols in which the leaching of the A horizon has been sufficiently active to cause a light gray color contrasting with the brown or red of the underlying B horizon. The rest are brown forest soils or transitions between them and the podsols, in which leaching has been less intense and the contrast between A and B horizons is slight or imperceptible to the eye. The numerous soil types represent too fine a degree of subdivision for analysis with the number of plots available. Therefore, for the study of soil-profile groups and relations, the plots were classified into 22 categories on the basis of observable profile characteristics. These were further condensed for certain purposes into 12 and 6 groups, always grouping those which had important characters in common. These groupings are believed to have significance but they do not correspond to any soil groups which have been described in the literature.

Soils develop under the influence of climate and vegetation. Although they change slowly, they are distinctly dynamic and not static in nature. Under certain conditions perceptible changes may take place within a human generation. Under others, changes are apparently very slight in many hundreds of years, and may even be comparable in rate with the changes in climate which have taken place in the 12,000 to 20,000 years since the melting of the glacial ice. Evidence of changes of this last order may be observed in the highly podsolized mature soils in which a gray podsol layer extends to a considerable depth. This development probably took place in large part during the period of cool, moist climate and vegetation of the succession to the Picea-Abies-Betula climax, following the retreat of the ice sheet. Subsequently the sharpness of the podsolic profiles has been dimmed, perhaps during the hypothetical xerothermic period, which was accompanied by invasion from the south and west (Gleason 1922).

On the western edge of the region, the duration of this period was sufficient for the formation of soil profiles with a dark-colored A horizon of mineral soil, high in organic matter from the excess of accumulation over leaching of the decaying roots of the grassland vegetation. Still more recently,

the climate seems to have become again more moist so that the deciduous
forest communities are tending to invade the grassland areas and arrest if not
reverse the process of prairie soil formation. But the change in climate has
not yet been sufficient to cause a further southward advance of the Picea-Abies
community. On the contrary, the evidence suggests that the deciduous forest
is advancing northward at the expense of the Picea-Abies community.

The significance of this movement in soil development lies in the bearing
which it has on the podsolization process. In northern Europe, raw humus is
associated with and considered actually to cause podsolization, and the vegeta-
tion which is charged with the formation of raw humus is that of the Picea,
Pinus, or more nearly arctic communities. Such species as *Vaccinium myrtil-
lus, V. vitis-idaea*,[4] *Calluna* spp., and *Cladonia* spp. are usually mentioned in
this connection (Tamm 1920). Here, these species or those most closely
related to them are characteristic of the northeastern conifer forest or of the
arctic communities and not of the deciduous forest. Furthermore, the asso-
ciated raw humus has not yet been found in this region if it occurs at all. The
conclusion is suggested that the podsol profiles commonly observed in the
aspen community are the result of an earlier period of cool, moist climate and
northern conifer forest vegetation, and that the podsolization process is not
active at the present time. In fact, as indicated by evidence brought forward
at the Harvard Forest in Massachusetts (Fisher 1928, Griffith, Hartwell, and
Shaw 1930), it seems likely that, under the influence of the deciduous forest
and present climate, the soil-forming process tends at present toward the
conversion of the podsol to the brown earth profile.

Vegetational History

The past history of the chief features of vegetational change just men-
tioned in connection with changes in climate and soil includes, first, a series
of successional stages from herbs through shrubs and forests of Pinus to the
climax of Picea-Abies-Betula under a cool moist climate; second, an invasion
of prairie and deciduous forest communities during a hypothetical xerothermic
period, and, third, the invasion of both prairie and northern conifer forest by
the deciduous forest stages leading to the *Acer saccharum*-Tilia climax. The
last process is continuing at the present time, if one may come to this con-
clusion from the prevalence of transitional communities with representations
of the species of both Abies-Picea-Betula and *Acer saccharum*-Tilia climaxes
in varying proportions. The subordinate arboreal and other plants of the
aspen communities sampled provide numerous examples of the early develop-
ment of the mixture of the two climaxes as well as of each of them separately.

A large part of the area of the aspen community in the region was oc-
cupied before human interference by one or the other climax forest, by the

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[4] Scientific names used throughout are from Rosendahl and Butters' "Trees and Shrubs of Min-
nesota" (1928) for the woody plants, and from Gray's Manual (1908) for other plants.

transition between them, or by a subclimax dominated by *Pinus strobus*. *Populus tremuloides* probably occurred as a dominant in limited areas and as an inconspicuous subordinate species in the climax forests wherever accidents or the death of large trees left openings. Logging and fires destroyed or eliminated most or all of the conifers, maple, and basswood. In the growing season following the fire, the bare habitat was densely occupied by a group of pioneer species composed chiefly of those which came from light and wind-borne seed and from the underground parts of the preceding generation. The commonest of this group are *Aralia nudicaulis, Aster macrophyllus, Betula cordifolia, B. papyrifera, Corylus rostrata, Diervilla Lonicera, Epilobium angustifolium, Fragaria virginiana, Populus tremuloides*, and *Solidago* spp. A large number of other species, relics which escaped the fires or those less efficient in their means of propagation, are more or less frequent associates. Among them all the aspen suckers lead in height growth from the first season. If the aspens are not sufficiently abundant to dominate the community after one fire, they are almost certain to do so after the second, third, or fourth fire.

After 10 years or more under the closed aspen canopy, the more mesic and shade-enduring species gradually invade, become established, and maintain themselves or increase in abundance and stature. Certain tree species grow under the aspen and, if undisturbed, form the next stage in the succession when the aspen dies between the ages of 50 and 100 years. The succession may take any one of several different directions depending primarily upon the environmental conditions. Most commonly it proceeds directly to the northeastern deciduous forest climax or to the northeastern conifer climax. On more xeric habitats, it may pass first to the *Pinus strobus* stage or even to a *P. resinosa* stage. On the hydric side, the succession is often to the Fraxinus-Ulmus-*Acer rubrum* stage or to Thuja or sometimes to a mixture of these two. There are groups of subordinate woody and herbaceous species which are more or less characteristically associated with each of these successions. They will be enumerated, classified, and discussed in some detail in a subsequent section. Before this is done it will be desirable to consider the work of others along similar lines.

PREVIOUS WORK

A certain amount of research has been carried out in the United States and Canada and in European countries on the relations between tree growth, soils, and vegetation by foresters and botanists with different points of view and objectives. Only a little of this work has included the interrelations of all three sets of factors, and still less has been concerned with the aspen community. These investigations, however, afford an interesting background, and insofar as they support or contradict the findings in the present study they tend to bring it into sharper relief.

RELATIONS OF VEGETATION, SOILS, AND GROWTH WITHOUT
REFERENCE TO ASPEN

A complete review of previous work including descriptions of all studies which might be considered to be related to the subject is not essential. A selection has therefore been made of those which seem most valuable or which are most nearly related to the subject of the present study. Other references to work on specific details will be included at appropriate places in the discussion, even though they may not be mentioned in this section.

From Cajander (1926) and his co-workers in Finland has come one of the most comprehensive expositions of a plant-indicator classification of habitats correlated with forest growth and soil properties, as a basis for the biological and economic evaluation of land productivity and use for forestry and other purposes. Although the categories of this classification go under the appellation of forest types, the words are used in quite a different sense from that usually given them in the United States. In Cajander's words,

"all those stands are referred to the same forest type, the vegetation of which at or near the time of maturity of the stands is characterized by a more or less identical floristic composition and by an identical ecologico-biological nature, as well as all those stands the vegetation of which differs from that defined above only in those respects which,—being expressions of differences due to age, fellings, etc.,—have to be regarded as merely accidental and ephemeral, or at any rate as only temporary. Permanent differences call forth a new forest type in cases where they are sufficiently well-marked, or a subtype in cases where they are less essential, but nevertheless noticeable."

The types are named after the most representative plant-indicator species in the typical communities but, in their identification, all the associated species of the community are taken into consideration. The communities in Finland are relatively few. They are made up of a small number of species which are surprisingly persistent under a wide variety of cover conditions. In this respect, the plant-indicator types are found to be more permanent than the forest cover, for both birch and Scotch pine, and sometimes also Norway spruce stands, may occur on the same "forest type." In a comprehensive study of growth and yield, including diameter, average and dominant height, and volume both per tree and per unit area, the types were found to be distinct and the differences between types greater than those within types, in all the respects in which growth was measured. It was concluded that the types are well-suited for the classification of soils and of site qualities for forest growth and yield. Table 2, taken from Valmari (1921), gives the essentials of these relationships, those for Myrtillus being taken as 100.

The figures in table 2 are based on averages of more or less variable individual determinations. Recently Aaltonen (1929) has admitted that the variations in the soil properties within the types are too great for satisfactory conclusions as to their relations to forest types and tree growth. The differ-

TABLE 2. COMPARISON OF RELATIVE TREE GROWTH AND SOIL CONSTITUENTS IN
IMPORTANT FOREST TYPES, ACCORDING TO VALMARI (1921)

Forest type	Relative current annual increments		Relative amounts in 8-inch surface layer of —	
	Scotch pine, Age 75	Birch, Age 60	CaO	N
Oxalis-Maianthemum	...	185	140	223
Oxalis-Myrtillus	115	117	117	137
Myrtillus	100	100	100	100
Vaccinium	83	83	79	71
Calluna	52	...	54	64
Cladonia	27	...	36	34

ence in the lime and nitrogen contents of the soils would almost certainly be associated with differences in soil profile types and surface formations if these had been included in the investigations. On the whole, this Finnish work provides strong evidence of a definite relation between plant indicators, tree growth, and soils.

The scheme was tested in the mountains of Germany by Bjorkenheim (1917), who concluded that Cajander's classification was applicable, with minor modifications, in Germany as in Finland. From 100 sample areas in the Picea forests, he found plant indicator types corresponding to different site qualities and average dominant heights as given in table 3.

TABLE 3. TYPE INDICATORS ASSIGNED BY BJORKENHEIM (1917) FOR DIFFERENT
HEIGHTS AND SITE QUALITIES

Type indicators	Dominant height	Site quality
	Meters	
Calluna-Cladonia	..	V
Calamagrostis	15	...
Myrtillus	19	IV
Aira	24	III
Oxalis	29	II
Afforested fields	..	I

An attempt to extend the Finnish scheme to the northern United States and Canada has subsequently been made by Ilvessalo (1929). His observations, chiefly in the forests of Pinus contorta in the West and of Pinus banksiana in the East, are admittedly insufficient for general conclusions. However, he sets up plant indicator types and finds that, as in Finland, they represent habitats upon which the growth of the forest as measured by the relation of dominant height and age, is, on the average, distinct. In the Pinus banksiana forests of Minnesota (Cloquet) and Ontario, the type is called Vaccinium-Gaultheria with probable sub-types, (a) Vaccinium-Myrica and (b) Vaccinium-Rubus-Papilionaceae. Many of the associated species are recorded from several or all of the types and sub-types. Moreover, the successional point of view, the fact that most of the shrubby and herbaceous species of the

forest are changing and will be replaced by others, is entirely ignored. This is a serious defect in a consideration of the two pine communities sampled in North America because both are single-generation pioneer forest stages in succession. The question inevitably comes to mind whether the scheme, at least in its application to our region, is not somewhat idealized, perhaps even to such an extent that its use would be difficult in many, if not a majority, of our forest areas.

The same basic idea of classifying lands for forest purposes by the vegetation and soils appears also in the recent investigations of afforestation in Great Britain by Guillebaud (1930). There the necessity for this basis of classification is acute because the lands have been deforested for years, perhaps centuries. For the same reason, the vegetation and soil types cannot yet be correlated with the growth of the trees. His soils and plant indicator types include grassland with Pteris on brown earth; heath land on podsolized sandy soils, often with shallow peat; and moorland, including the Molinia and Nardus communities on boulder clay and the deeper peats which are subdivided into Juncus peats, Molinia peats, *Eriophorum vaginatum* L. peats, *Scirpus caespitosus* peats, and mixed types containing Calluna. These types are found to be very different in their suitability for drainage and forest planting.

An interesting attempt to devise a soil classification and show its relation to forest types and site qualities has been made in Latvia by Kirstein (1929). The main divisions are based upon the character of the substratum, as marly loam, sandy loam or gravel, sand, and swamp. The first three groups are each subdivided into four according to amount of lime, physical condition, reaction of the mineral soil, and thickness of the humus horizon. The swamp soils are grouped into four categories according to their acidity. Each of the foregoing subgroups is finally classified as to its prevailing moisture content into dry, moist, periodically wet, and wet. Some of the possible categories in this classification are never filled. For example, there are obviously no dry swamps. Nevertheless, the method is relatively simple and is based on a combination of the most reliable and easily determined soil properties.

To a considerable extent, the forest types, characterized by the predominating tree species and the site qualities on a productivity scale of I to V, were found to correspond specifically with these categories. Insofar as this is true, the classification makes it possible to determine the natural forest type and site quality, even in the absence of forest cover, by observation of the soil profile and determination of acidity and lime content. A few of the soil classes, however, represent transitional stages in the forest and are therefore not specific. For example, a moist sandy soil, low in lime and acid in reaction with poor structure and thin humus, may have either Pinus or Picea forest of site quality II or III. Occasional instances of this kind would be almost inevitable in a classification based on the soils. Conversely, the same forest

type and site quality may be found in more than one of the soil categories. Thus, site quality I for Picea-Quercus forest may be on moist, neutral, marly loam with ample lime; or on moist sandy loam, high in lime and neutral in reaction; or on moist sand, high in lime and neutral. Although this investigation did not include the plant indicators, it appears to be quite satisfying for the relations between soils, forest types, and their productivity in a limited region.

A somewhat different line of attack was made in Germany by Barth (1928). He selected areas of the Quercus community representing five different site qualities based on a comparison of average height of stand with yield table values. Profile descriptions and soil samples at three depths were taken and analyzed for texture, water capacity, air capacity, hardness, organic matter, nitrogen, SiO_2, Fe_2O_3, Al_2O_3, CaO, MgO, K_2O, and pH. The soil profiles were distinct from one another in several respects, among which degree of podsolization as indicated by the degree of leaching in the upper horizons and the formation of ortstein in the lower should be mentioned. The conclusions were as follows: In soils of high moisture content, the closest relation to site quality or productivity is found in the air capacity, lime content, and reaction; the height-site qualities of yield tables are only average values and are not always applicable to specific habitats; the associated vegetation serves to indicate changes between adjacent habitats chiefly by changes in the relative abundance of the common species for those particular habitats and the absence or appearance of less common species. Although this study was concerned primarily with soil properties rather than soil types, it has a special interest because it is limited to those changes in environment which may be related to growth within a single forest community, the same limitation that is imposed by confining the present discussion to the aspen community.

In Sweden, vegetation and soil types have been studied and correlated by Tamm and Malmström (1926), although they have not yet introduced the growth or productivity factor into the correlations. The point of view has been the practical one of indicating differences in habitats which correspond to differences in the forest and accordingly require special silvicultural treatment. The other noteworthy feature of the Swedish work in comparison with that of other European countries is the recognition given to the dynamic and changeable character of both vegetation and soil types. In the former respect, the succession after fires has been shown to pass from Betula and Pinus to Picea; in the latter, the time for the development of the podsol profile has been quite definitely established as between 100 and 1,500 years, depending upon the vegetation and environment. Furthermore, Tamm (1920) has shown that the different vegetation types, by means of the humus produced, influence markedly the rate at which leaching and podsolization proceed.

The most recent summary of the soil types and vegetation by Tamm (1930) summarizes the types as follows: The two main divisions are podsols

and brown earths. The latter, limited in Sweden to the southern part, have deciduous forest, and on the moraines chiefly Fagus with the herbaceous plants, Anemone, Hepatica, and Oxalis. The podsols include soils with mull or mild humus and deciduous forest; soils with raw humus without ortstein, having Vaccinium-rich or lichen-rich pine forests; soils with raw humus and with ortstein, having Calluna heath or, in the north, conifer forest; and humus podsol soils, having sphagnum-rich heaths or forests of spruce and also pine and birch of the Dryopteris type. The vegetation classification of Tamm and Malmström (1926) is much more detailed than that of the soil but, lacking the soil equivalents, no useful purpose would be served by reviewing it.

The plant-indicator type idea has been applied to the Danish beech forests by Bornebusch (1931). He distinguishes basic types as the equivalents of the Finnish forest types, which have different soils and cause different flora types within the beech forests. These types are (1) Circaea type, on brown loamy or clayey, high-lime, marl soils with mull and pH, 5.5 to 7.0; (2) Corydalis type, on deep mull soils,—the best sites for beech, which there grows to a height of 30 meters; (3) Mercurialis type, soils more moist and low, good sites for beech; (4) Circaea-Asperula type, somewhat low sites, medium for beech; (5) Primula or Ficaria type, low flat moist sticky soils, poor growth of beech; (6) Anemone-Asperula type, loamy sand and gravelly soils, mull not influenced by limey C horizon, average site for beech; and (7) Oxalis type, degraded brown earth soils with raw humus, gray A_2 horizon and mull of pH 4.0 to 5.5. Additional plant indicators are enumerated for each type but very few of them or of the type species seem to be characteristic exclusively of a single type. *Circaea lutetiana* is listed in 1, 4, and 5, *Anemone nemorosa*, in 2, 3, 4, and 5, Mercurialis, in 2 and 3, Oxalis and Veronica in 4 and 7, and similarly with most of the species. The two interesting things in this study are the lack of specific indicator value of individual species by themselves and the possibility of differentiating useful groups of plant-indicator types with corresponding soil and site-quality differences within a single forest community.

A thorough classification of so-called "forest types" in Russia has been made by Krudener (1927). He defines his forest types as definite plant communities which have developed under given climatic, soil, and underground conditions. Further, the principal soil and geological formations, typical soil and subsoil conditions in relation to soil moisture, aeration, and the character of the organic surface horizon—in connection with the mineral substratum and parent material and in the presence of a definite shrubby and forest community—give definite micro land classes or forest types. His approach to the plant community or forest stand, therefore, is through the environment, climate, and soil. Theoretically, he discusses the different orders of subdivision: First, the climatic and physiographic regions; second, within each, the mineral substrata, whether sandy, loamy, or stony, and their water

regime; third, the soil types, including such categories as plant and plant-mineral layers, black earth, humus carbonate, humus layers of mould, mull, and raw humus, and the alluvial silt and peat deposits with excessive moisture. Actually the "forest type" classification is one of soil types in which hygrometric groups, organic or mineral substrata, soil moisture, aeration, and character of the upper organic horizon are combined with petrographic, physico-mechanical groups into 15 types. The correlation of these types with forest composition is indicated to some degree, but less clearly with site qualities. Thus, although the soil and habitat classification is exceedingly thorough, the resulting categories in many instances are not distinct either with respect to the actual forest cover or to the productivity of any given kind of forest. At the same time some of the soil types include site qualities with ranges as wide as I to III or IV to VI. Again it appears that a classification based on soils does not correspond in its categories to specific forest types and site qualities.

One of the most interesting and complete plans for the classification and correlation of habitats, forest growth, and plant indicators has recently been made available in German by Pogrebnjak (1930). It is based on the work of Alexejew in the Ukraine. The habitat classification is constructed from two features of the soil—the mechanical (petrographic) composition and the depth of the ground water. The former, in effect the chemical fertility of the soil, is divided into six degrees to form graduations along a horizontal scale from low through rich to "excessive" (in alkali soils). Similarly, different levels of the ground water correspond to six graduations of a vertical scale from very deep at one extreme to very shallow or surficial at the other. The latter scale corresponds closely to the range from xeric to hydric. The two scales are combined as coordinates in a diagram on which the distributions of the species of trees and plant indicators and of the site qualities of the forest stands are outlined to form what is termed an ecofigure. Each species or productivity class thus forms a closed area on the diagram, the perimeter indicating the limits of distribution as determined by soil fertility and moisture, and the center the optimum for that species or class. In this way the inter-relations of species or communities and growth rates may be compared visually with one another in respect to their responses to fertility and moisture which define the habitat categories. The scheme obviously requires a thorough knowledge of certain key trees and plants in relation to their habitats for its initial construction but, once constructed, it effectively coordinates habitats, plant indicators, and forest productivity.

In the United States, the relations between soil and forest growth have been studied by Haig (1929) and (in Connecticut) by Morgan (1930). They both used the site index of Norway pine plantations as the measure of soil productivity and have correlated that with certain soil properties, types, and classes. Some preliminary work with the natural mixed hardwood forests and the soil types as mapped by the Bureau of Soils proved disappointing. Sub-

sequently Haig found significant correlation indices between the Norway pine site index and soil conditions, as follows: Colloidal content of the A horizon, 0.52; colloidal content, A and B horizons, 0.55; silt plus clay, A horizon, 0.58; and colloidal content plus organic matter plus reaction, A horizon, 0.65. Correlation with soil class was 0.70, and with soil type 0.80. Sufficient data were not available for an adequate investigation of the soil type correlation but it is suggestive that the soil type, which integrates all of the soil factors, seemed to be more closely related to tree growth than any of the individual soil properties or lesser combinations of properties.

Additional work is reported by Morgan to the effect that the moisture equivalents of the A horizon show a somewhat better correlation with site index than the texture, that no definite correlation could be established with the soil reaction, and that a suggested correlation was found with the replaceable calcium of the A horizon. Low transformation of nitrogen into ammonia and nitrates was associated with low site index. High site indices occurred on soils which showed a tendency to form a raw humus layer, although in general the soils with active earthworm mull were slightly superior.

The plant indicator concept, in relation to soil types, agricultural productivity, areas for afforestation, and forest communities, has already a considerable literature which is well known. The works of Hilgard (1906), Shantz (1911), Korstian (1919), and Clements (1920) do not require detailed review. Korstian called attention specifically to the probable value of plant indicators of different site qualities for the growth of trees and cited the example of *Pinus ponderosa* in New Mexico where site I with mesic species produced 64 percent more increment than site II to which certain xeric species were limited.

Recently Holman (1929) in Alberta has enumerated the ground vegetation characteristic of each of three site qualities as determined from the rate of growth in pure forest sample plots. Brief notes of the humus conditions do not sufficiently characterize the soils. Many of the plants, however, belong to the same genera as those to be presented hereafter and are therefore of some interest. They are tabulated below in parallel columns. Site I is the best and site III the poorest.

SITE I	SITE II	SITE III
Actaea	Alnus	*Antennaria microphylla*
Alnus	Fragaria	Arctostaphylos
Coptidium	Ledum	*Hedysarum sulphurescens*
Corylus	Mertensia	*Juniperus siberica*
Heracleum	Moneses	*Sabina horizontalis*
Mitella nuda	Petasites	*Zygadenus elegans*
Oxalis	Pyrola	
Pteridophyta	Rosa	
Ribes	Salix (dwarf)	
Salix	Shepherdia	
Smilacina	*Vaccinium* spp.	
Viola	*Vaccinium vitis-idaea*	

The relation of natural vegetation to soil types and their acidity has been investigated for six soil types in Pennsylvania by Kelly (1922). The soil types, their pH and the characteristic plants, including only those also found in this study, are given below.

Soil Type	Characteristic Plants
Hagerstown loam (pH 7.2)	*Quercus alba, Fraxinus americana, Corylus americana, Celastrus scandens, Equisetum hyemale, Asarum canadense, Aquilegia canadensis, Mitella diphylla.*
Manor Valley loam (pH 7.2)	*Ostrya virginiana, Prunus pennsylvanica, Fraxinus pennsylvanica lanceolata, Osmunda cinnamomea, Lycopodium annotinum, Trientalis americana.*
Conowingo loam (pH 7.1)	*Acer rubrum, Andropogon scoparius.*
Chester loam (pH 7.0)	*Quercus rubra, Ulmus americana, Prunus americana, Fraxinus americana, Amelanchier canadensis, Smilax herbacea, Iris versicolor.*
Manor loam (pH 6.6)	*Carya cordiformis, Betula lenta, Viburnum acerifolium, Pteris aquilina, Viola pubescens.*
Dekalb loam (pH 6.2)	*Amelanchier oblongifolia, Symphoricarpos, Iris versicolor.*
Manor stony loam (pH 5.7)	*Epigaea repens.*

Many other species, occurring on most or all of the soil types, were not considered characteristic. The differences between soil types are not striking and it may even be questioned whether the characteristic species would have continued to be characteristic, if a larger number of sample areas of each soil type had been examined.

After studying in considerable detail the properties of four soil types on the Mont Alto State Forest in Pennsylvania, Auten (1930) concluded that volume growth of wood was independent of soil texture and had no perceptible relation to total nitrogen, phosphorus, or calcium or to the microorganisms present. Aspect and exposure, in their influence on soil moisture, were found to cause differences in floristic composition and as much as 100 percent difference in volume increment as between cool moist and dry exposed sites "on the same soil type." It seems possible that a difference in soil type may have existed in situations of such contrasting character. However that may be, the change in volume growth with difference in habitat is clear, and in addition there is a difference, not in the plant indicators within a community, but in the tree dominants themselves.

The phytometer method has been much used in ecological investigations by Clements and Goldsmith (1924), Clements, Weaver, and Hanson (1929), and others. It has been proposed for, and would seem to be well suited to, the study of plant growth as a measure of habitat; but for some reason it has

been little used in the measurement of soil productivity, unless the measurements of growth in forest communities be considered as examples of free phytometers. In that sense, the plots of the aspen community may be considered as phytometers.

ASPEN GROWTH, ASSOCIATED VEGETATION, AND HABITATS

Only a small proportion of the comparatively little work that has been done in the aspen community covers the relation between aspen growth, associated vegetation, and habitat. In northern Europe, Schotte (1916-17) found *Populus tremula* on two distinct sites, one producing 200 and the other 150 cubic meters at 50 years. They were also distinct in respect to vegetation and soil. Eklund and Wennmark (1925), supplementing Schotte's work in Sweden, found that the height of the aspen appeared to be specially affected by the character of the soil, which they considered to be the dominant factor. At 50 years on site quality I the height of the aspen was 68 feet and on site II, 56 feet, with corresponding differences in volume growth.

In the United States, a study of aspen in New England by Weigle and Frothingham (1911) showed marked differences in growth on different sites. The heights at 50 years were 75 feet on site I, 65 feet on site II and 50 feet on site III, but these sites were not described as to their soils or associated vegetation. In the Central Rocky Mountain region, Baker (1925) distinguished 5 sites for aspen on the basis of the height of dominant trees at 50 years and briefly characterized the habitat of each site quality as follows: Site 1, height 57 feet, on moist flats with deep, rather heavy soil; site 2, height 48 feet, less well watered than 1 and more often on slopes; site 3, height 37 feet, similar topography to 2, but below the optimum altitudinal zone for aspen; site 4, height 30 feet, at the lower limits of the type and on south slopes at higher elevations; site 5, aspen of unmerchantable thicket type, on poor soils of south and west slopes, particularly above the zone of best development. Baker notes that there is extremely close correlation between height and annual volume increment as criteria of site, and the foregoing habitat descriptions indicate relationship between growth and habitat, although not in terms directly comparable with any of the soil classifications used in the present study.

A detailed frequency analysis of the vegetation of the aspen community in northern Lower Michigan has been made by Gates (1930). He classifies the species in three categories, pineland, hardwood, and lowland, which correspond to different habitats, namely, dry sandy upland, moderately moist loamy upland, and moist lowland, but these habitat categories are rather broad and no correlation is made with the growth of the aspen. His analysis shows, however, that the habitats may be distinguished by the composition and frequency of occurrence of the associated species in the aspen community.

Earlier, in the same vicinity, the associated species of the aspen community

were studied in connection with the theory of species and area by Gleason
(1925). After computing frequencies for the different species on different
combinations of quadrats, he concluded that "environmental differences in the
aspen association, while observable, are not of sufficient magnitude to affect
the distribution of the species," and again, "within the limits of a single plant
association, the environment, while possibly presenting observable differences,
is essentially homogeneous for each species." His quadrats, however, were on
level terrain in a soil of almost pure sand in which repeated tests of soil acidity
failed to show any variation. A wider sampling of the aspen community
might have modified these conclusions. It will be interesting to compare these
statements with findings in the later section on plant indicators in relation to
habitat.

The growth of aspen, including the preparation of site-index curves, has
been analyzed in considerable detail by Kittredge and Gevorkiantz (1929),
largely on the basis of the data of the present study, but with little considera-
tion of habitat and plant-indicator relations. There is no reason to review
those findings, since much more complete and critical analyses of the same
material are made in the following sections.

ANALYSIS OF GROWTH RATE
POSSIBLE MEASURES OF TREE GROWTH

Features which, observed over a known period of time, provide a measure
of tree growth rate include dry weight, leaf area, crown dimensions or volume,
stem dimensions or volume, and heights of all or of the dominant trees.

Dry weight is ordinarily considered, and logically so, to give the best
measure of growth, because it includes all of the dry matter produced by the
plant reduced to a standard moisture content. Total leaf area gave results
corresponding closely to those by dry weight in the work on competition by
Clements, Weaver, and Hanson (1929). But neither of these features pro-
vides a measure of growth for trees of greater bulk than 15-year-old trees.
Crown diameter and length may be measured rather closely and may be com-
bined to obtain crown volume, which supposedly would give values com-
parable to leaf area. But this measure becomes almost prohibitive when 20 or
more trees on each of 277 plots are concerned. Moreover it would be par-
ticularly susceptible to variation with differences in density of the stands, and
thus differences due to soil productivity would be obscured.

Lengths of the stems or total heights and diameters at 4½ feet above
ground are readily measured on sample trees and when combined with a form
factor express quite accurately the volumes of the stems. This is the measure
of volume and growth commonly used by foresters in all countries. Although
its use is dictated in part by reasons connected with utilization of the wood,
there is no reason to believe that, for any given species of relatively uniform
crown development like aspen, it is not at least closely correlated with dry

weight and leaf area. Stem diameters and volumes, however, are also subject to wide variations with differences in density.

Finally the heights of the taller or dominant trees, which receive full light from above and some from the sides, may be averaged to provide a measure of growth. Since height growth in well-stocked stands, or stands in which the density factor is relatively constant, has been shown by Gevorkiantz and Zon (1930) to be a linear function of volume growth, this characteristic may be used in place of volume growth. It has the advantage, as compared with volume growth, that it is influenced less by changes in density and this influence is minimized if the heights are limited to those of the dominant trees. It has frequently been observed in height measurements of forest trees of the same age that those growing in the open and those in very dense groups are shorter than those in stands of moderate to well-stocked density. The same thing is proved in the controlled experiments of Clements, Weaver, and Hanson (1929) with Helianthus, Xanthium, Triticum, and Andropogon. They grew cultures with the plants spaced uniformly at intervals of 2, 4, 8, 16, 32, and 64 inches. Heights reached a maximum with the 4- or 8-inch spacings and decreased somewhat as the densities were either greater or less than these. Thus, although height growth is not a reliable measure of productivity in either extremely dense or extremely open stands, it probably is more reliable than any of the other measures over quite a range of intermediate densities, such as are represented by most of the plots in this study. Stem volume growth and height growth of dominant trees have both been used in this study and further comparisons of them will accordingly be made.

STEM VOLUME GROWTH PER UNIT AREA

The components of stem volume as a measure of growth rate are diameter, height, form, age, and density. From the direct measurements of diameters and heights of sample trees, curves of height over diameter were drawn for each plot and the values read from these curves were used for the heights of the trees for which only diameter measurements were available. The volumes were then read from volume tables based on diameter and height, already available. The preparation of the volume tables makes allowance for the factor of form of the stems (volume $=$ diameter^2 $\times$ height $\times$ form factor) insofar as it varies with diameter; height and further variations due to age or density within any given diameter and height class are believed to be negligible or at least well within the limits of error to which some of the other data are subject. Density, expressed as number of aspen trees per acre, cannot be ignored when using volume growth as a measure of productivity. Accordingly it seemed essential to limit the application of the volume growth criterion to a group of plots in which the density was relatively uniform. This was done by separating the well-stocked from the understocked and overstocked plots and using only the well-stocked in the measurement of productivity. This separa-

tion on the basis of density appears somewhat involved where plots of different
ages growing on different soils are concerned because these are themselves
factors affecting density.

As a first step, the values of number of trees per acre were plotted over
mean diameter for each of the 248 plots (fig. 2). It may be seen that the
number of trees per acre decreases very rapidly as the mean diameter increases
from 1 to 3 inches, more gradually from 4 to 9 inches, and very slowly from
9 to 15 inches. The two coordinate axes tend to form asymptotes to the two
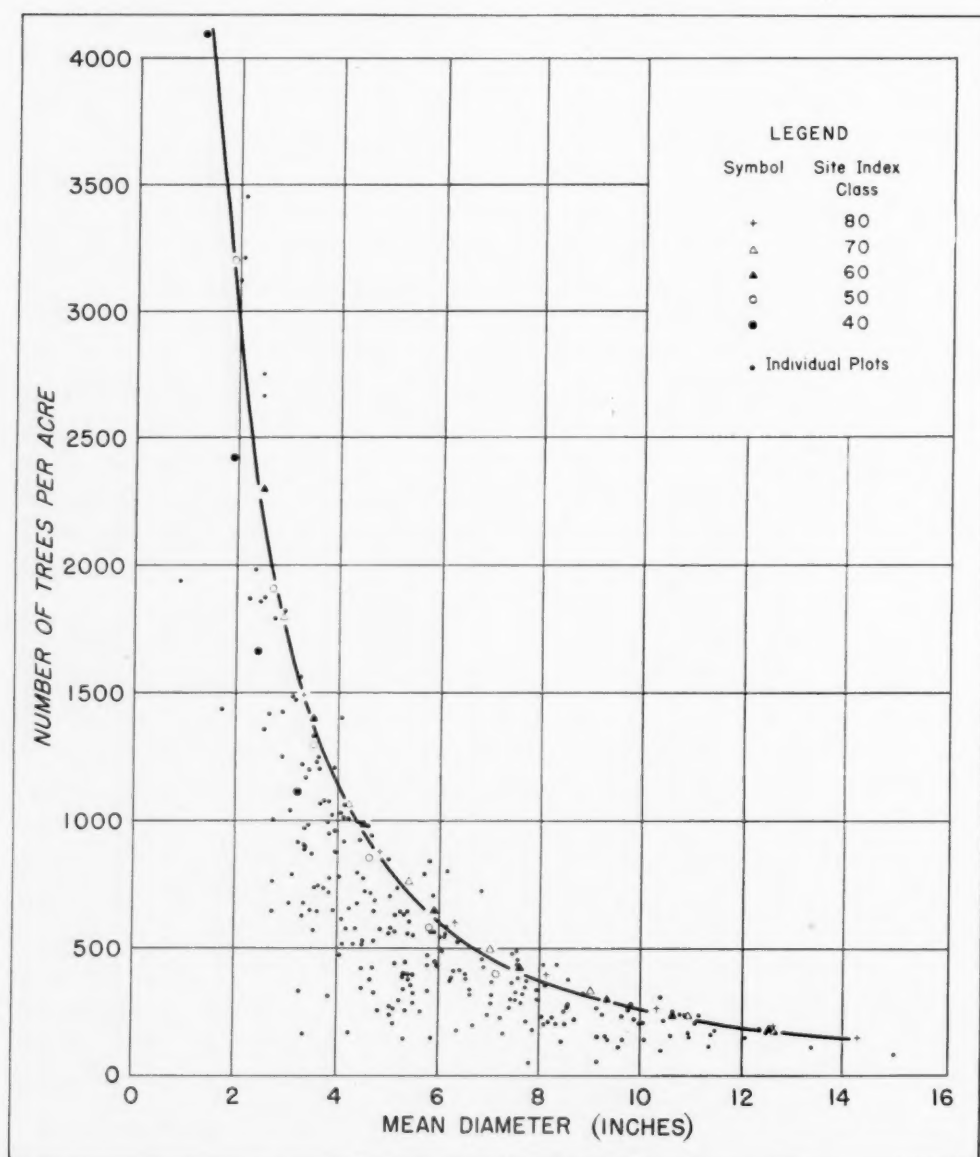
FIG. 2. Relation of number of trees per acre to mean diameter. The dots represent
plotted values for each of 248 plots; the symbols represent the smoothed averages of age
and site-index classes, as obtained from 103 well-stocked plots.

ends of the trend, and this, with the general form, suggests that it may be represented by a hyperbola. As a preliminary test of this possibility, the average figures for numbers of trees per acre and mean diameter derived from the 103 well-stocked plots, previously segregated by means of the relation of basal area[5] to age and site index (Kittredge and Gevorkiantz 1929), were also plotted and a smooth curve drawn through them. The trend of the points is strongly and closely defined. When values read from this curve were then plotted on logarithmic paper, they formed a straight line (fig. 3, line F–F), thus confirming the suggestion that the relationship could be represented by a hyperbola.

It may be observed that the excellent alinement of these points was obtained in spite of the fact that they represented different site-index groups and different ages. This confirms the conclusion of Gevorkiantz and Zon (1930), who refer to the idea of Russian workers, that the relation of number of trees per acre to average diameter is independent of age and site quality. This relation is reasonable from biological considerations. Assuming a specified area of ground, its full productive capacity may be utilized either by a small number of large trees or by a large number of small trees, provided the trees are growing in pure, even-aged stands. Any increase in the size of the trees due to greater age is associated with mortality of the weaker individuals and reduction in the number of trees on the area. Similarly, on a good site as compared with a poor site, the individual trees grow larger but the number of them which can survive is not as great. If the stand is very dense at the start, the diameter growth of the trees will be retarded but their number per unit area is greater. The separation of cause and effect in this relation is not always easy, but its reciprocal nature and its independence of age and site quality, which are expressed in the mean diameter, seem logical.

Finally, the values of average diameter and number of trees per acre for each plot were also plotted on figure 3, separating those for the well-stocked plots from the others. The points representing well-stocked plots are concentrated along the trend line while most of the others fall considerably below it. This relationship, therefore, seems to offer a check or alternative method for the division of stands on the basis of stocking or normality. Deviations to the left or below the straight line trend formed by the upper band of points on the logarithmic paper would result when a stand had any combination of subnormal number of trees per unit area with subnormal diameters. Such a combination might be due to competition of other species in the stand, or to suppression of some or all of the aspens by larger trees of other kinds, or to early suppression of the aspen by trees which were subsequently cut. Stands which had been subject to any of these influences would evidently require careful scrutiny before they could be considered reliable as indicators of soil

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[5] Basal area $= \Sigma(\frac{\pi}{4}d^2)$ per acre.
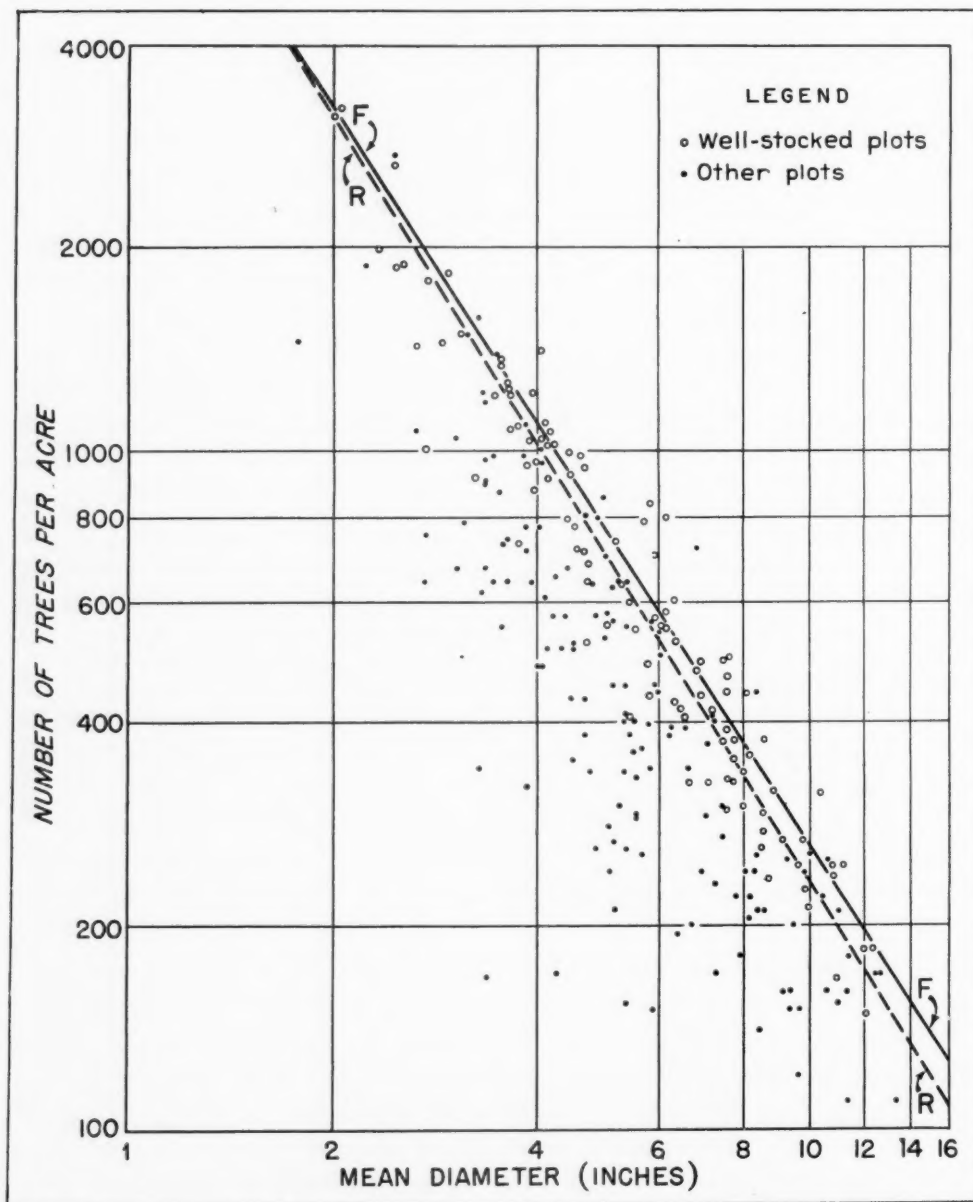
FIG. 3. Determination of hyperbolic relationship of number of trees per acre and mean diameter. Line F-F connects smoothed average values plotted from the curve in figure 2. Line R-R is a regression line plotted from the formula $\log D = 2.44 - 0.61 \log n$.

qualities. Deviations on the side of the curve toward the origin would also result (and probably more commonly) when insufficient seed or parent roots at the time of establishment caused the number of trees per acre to be sub-normal. In such cases, even though diameters would tend to be abnormally large, a young stand with few trees per acre would not immediately put on diameter increment sufficient to maintain the normal relationship between

diameter and number of trees per acre. For example, suppose that only 200 trees per acre appear after a fire. The normal diameter for a stand of 200 trees per acre is about 11 inches. Evidently, however, these 200 trees cannot possibly attain diameters of 11 inches for 40 or 50 years. During the intervening period, the stand will be judged subnormal by the criterion of *diameter-number of trees per acre*.

In order to establish a standard of normality in respect to the relation between diameter and number of trees per acre, a straight line was fitted to the logarithms of the values of the 103 plots which were judged to be well-stocked by field observations. The general equation of a hyperbola when there is no constant term is $y = ax^{-b}$ or for these data, $D = an^{-b}$. In logarithmic form this becomes, $\log D = \log a - b \log n$, which is the equation of a straight line on logarithmic paper. The two normal equations by the method of least squares then are,

$$\Sigma \log D = N \log a - b \, \Sigma(\log n)$$
$$\Sigma(\log n) \, (\log D) = \log a \, \Sigma(\log n) - b \, \Sigma(\log n)^2.$$
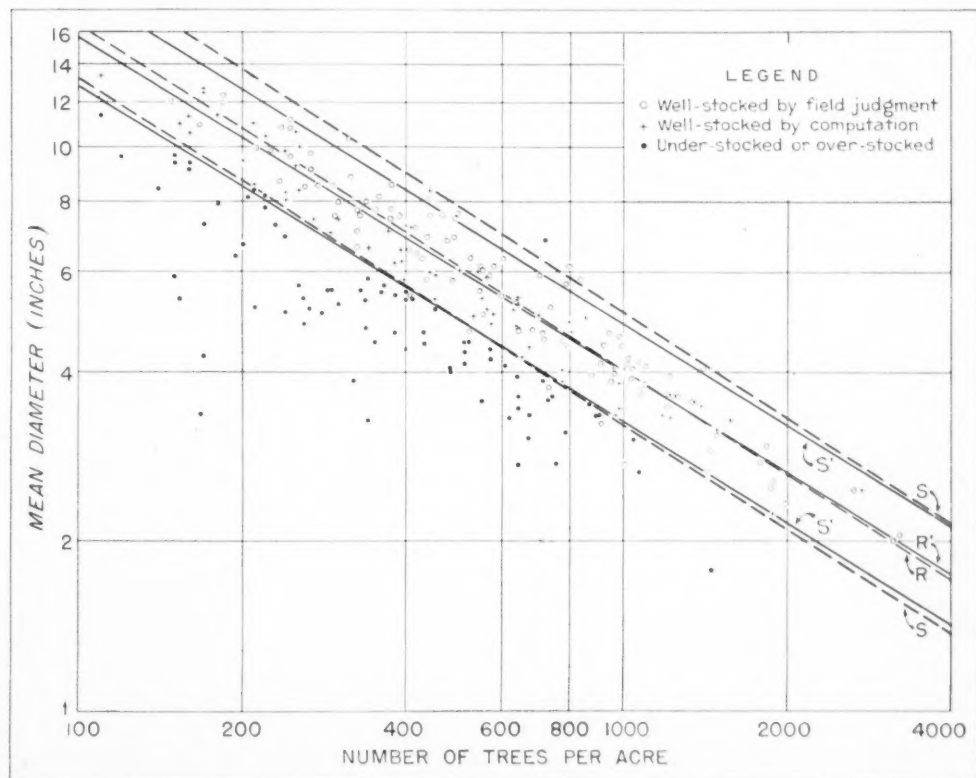
FIG. 4. Plotted points from figure 3, with line R–R. S–S is a band defining the limits of twice the standard deviation about the line R–R. The line R'–R' is a new regression line, $\log D = 2.38 - 0.59 \log n$, calculated by the inclusion of the 58 plots, originally recorded as poorly stocked, that lie within the band S–S. S'–S' is the new band based on R'–R'. Nine plots included in S–S are rejected by S'–S'. (Although the variables as presented in figure 3 are interchanged, the equations in every case represent the regression of log diameter on log number of trees.)

Computing, summing, and substituting the values in these two equations, they become,

$$75.7039 = 103 \log a - 287.4251 \, b$$
$$205.6132 = 287.4251 \log a - 811.3025 \, b.$$

A solution of these two simultaneous equations gives $b = 0.6105$ and $\log a = 2.4386$. These two values substituted in the original logarithmic equation give

$$\log D = 2.4386 - 0.6105 \log n$$

which is the equation of the regression line of $\log D$ on $\log n$.

This line is plotted in both figures 3 and 4 as R–R and obviously fits the trend of the 103 well-stocked plots. Although it does not coincide with the line previously plotted, derived from the relation between basal area and age for the same plots, the two diverge so slightly that either one might be used as a criterion of normality of stocking. The relation between diameter and number of trees per acre is much easier to obtain, since it involves only one set of measurements and counts and avoids the computation of basal areas and the determination of age.

The standard deviation (S) about the line of regression was obtained from the relation—

$$r = b_{\log D \log n} \left(\frac{\sigma_{\log n}}{\sigma_{\log D}} \right),$$

where

$$\sigma_{\log n} = \sqrt{\frac{\Sigma(\log n)^2}{N} - M_2 \log n} = \pm 0.2996$$

and

$$\sigma_{\log D} = \sqrt{\frac{\Sigma(\log D)^2}{N} - M^2 \log D} = \pm 0.1897$$

then

$$S_{\log D} = \sigma_{\log D} \sqrt{1 - r^2}.$$

If, thus,

$$r = 0.964$$

and

$$S_{\log D} = \pm 0.0504,$$

then, $2S = \pm 0.1008$. This may be interpreted to mean that, in 95 cases out of 100, another well-stocked aspen plot selected from the same range of environmental conditions would, with respect to its relation between average diameter and number of trees per acre, lie within 0.1008 logarithmic units of diameter above or below the regression line. The two lines representing this range are also plotted on figure 4 forming the band S–S. It may be observed

that, of the 103 well-stocked plots on which the calculations were based, only 7 lie outside this band, 2 above and 5 below, or 96 out of 103 lie within, as compared with the theoretical 95 out of 100.

In addition, 58 of the plots designated in the field as not well-stocked lie within this band. If the 103 plots were insufficient to serve as a basis for the band, these additional plots could be included to make up the deficiency. It may well be questioned, however, how much they would actually modify the band's slope or width.

Certainly, continued repetitions of the process of rejection and recomputation would gradually cause the narrowing of the band until only those values remained which lie on the regression line and would therefore be absurd. Only one repetition with the additional plots was made in this case. For this purpose, all the plots lying within twice the standard deviation about the regression line were used to recalculate a new regression line and new band. With $N = 161$, the formulae are identical with those previously used. The values obtained are,

$$b_{\log D \log n} = 0.5913$$
$$\log a = 2.3762$$

and the regression equation is

$$\log D = 2.3762 - 0.5913 \log n$$
$$\sigma_{\log n} = 0.3105$$
$$\sigma_{\log D} = 0.1888$$
$$r = 0.973$$
$$S_{\log D} = \pm 0.0435$$

and

$$2S_{\log D} = \pm 0.0870$$

This line and its band are plotted in figure 4 as $R'-R'$ and $S'-S'$. This line is slightly lower and has a little less slope than the first line and the band represented by $2S$ is narrower, the lower limit nearly coinciding with the former position and the upper limit somewhat lower throughout its length. Thus one additional plot below and eight above are rejected as being understocked and overstocked respectively. The remaining 152 plots will be considered normal in respect to the relation between diameter and number of trees per acre in any analysis where it seems essential to have uniformity in these characteristics.

THE AGE OR TIME FACTOR

In order to use the volumes or heights of plots of different ages as a measure of the habitat differences, it is obviously necessary to eliminate or hold constant the age variable. This may be done conveniently by the process of anamorphosis in the same way that Bruce (1923) has suggested its use in the

elimination of age in the preparation of a site-index scale based on dominant height. First the volumes of the 161 well-stocked plots are plotted over age in figure 5. As the trend is evidently not far from linear, the regression line
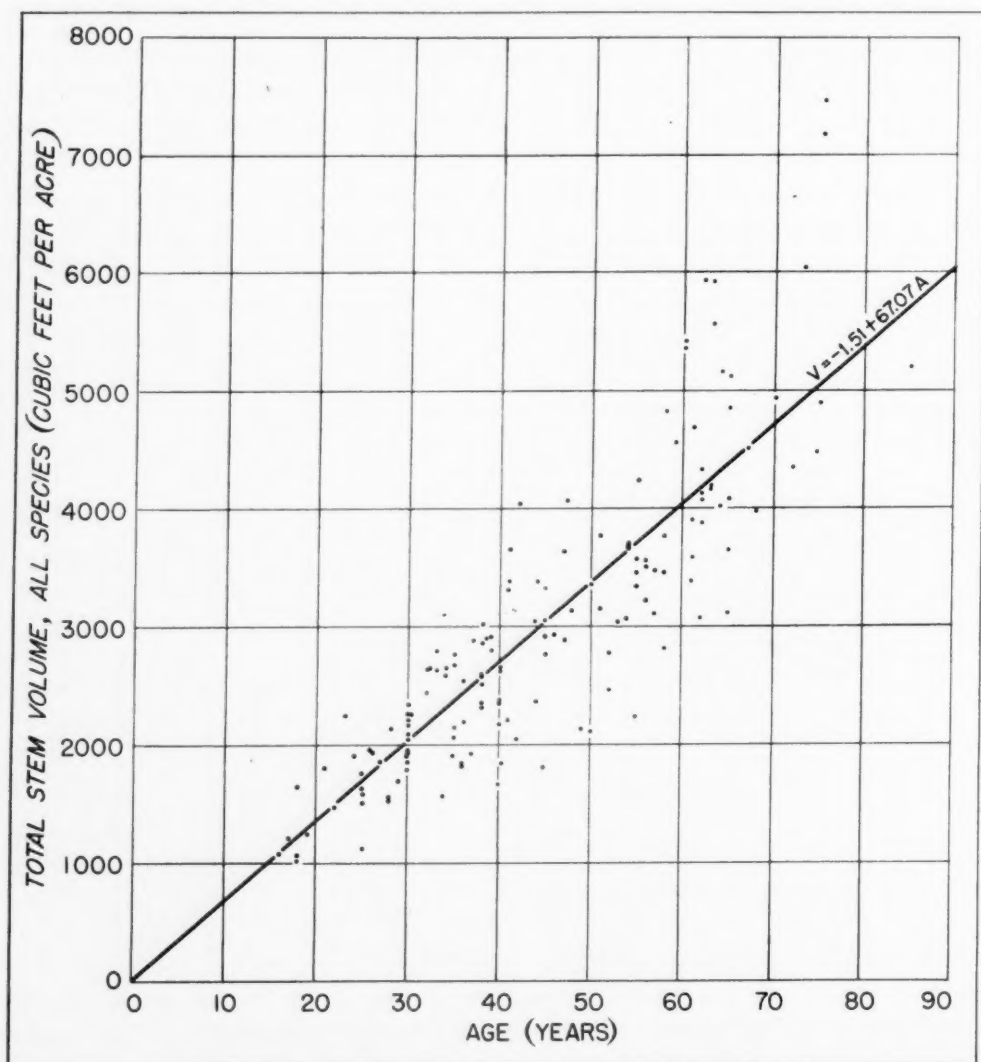
FIG. 5. Relation of volume to age in well-stocked stands.

of volume on age is fitted by the method of least squares. The equation of the line is: $v = a + bA$ when v = volume and A = age. The normal equations then are $\Sigma v = Na + b \Sigma A$, and $\Sigma vA = a \Sigma A + b \Sigma A^2$. Substituting the values, these become,

$$480,871 = 161a + 7,173b$$
$$23,994,306 = 7,173a + 357,751b.$$

Solve the two simultaneous equations, $b_{vA} = 67.073$ and $a = -1.51$, and the regression equation becomes $v = -1.51 + 67.07A$, or the straight

line plotted in figure 5 with its origin close to zero. The volume index is shown in figure 6, where the volume at 50 years is taken as a common denominator. The volume index for any plot is obtained by locating it in this
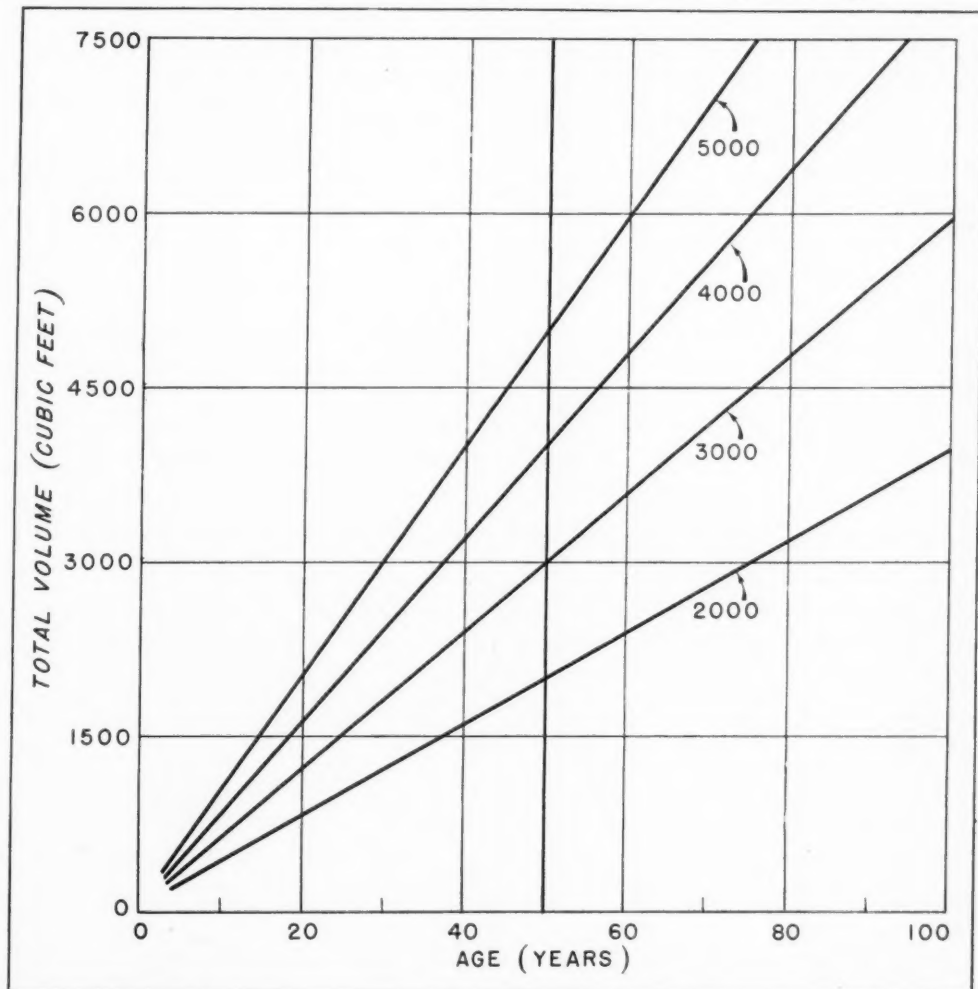
FIG. 6. Volume index for aspen, based on relation of volume to age in 161 well-stocked stands.

new set of coordinates, according to its volume and age, extending the line from the origin through this point to its intersection with the 50-year abscissa, and reading the volume index corresponding to this intersection on the volume scale at the left. Thus every plot of whatever age is expressed in terms of the volume which it would have if it were just 50 years old, and the age variable is held constant. The pencil of lines in figure 6 are those for the even thousand volume indices.

SITE INDEX FOR ASPEN

A series of site-index curves for aspen had previously been prepared by the same process of anamorphosis just outlined for the volume index. These

curves, with an explanation of their use, are available in the publication by Kittredge and Gevorkiantz (1929). For convenience of reference in the present study, they are reproduced in figure 7. They differ from the volume
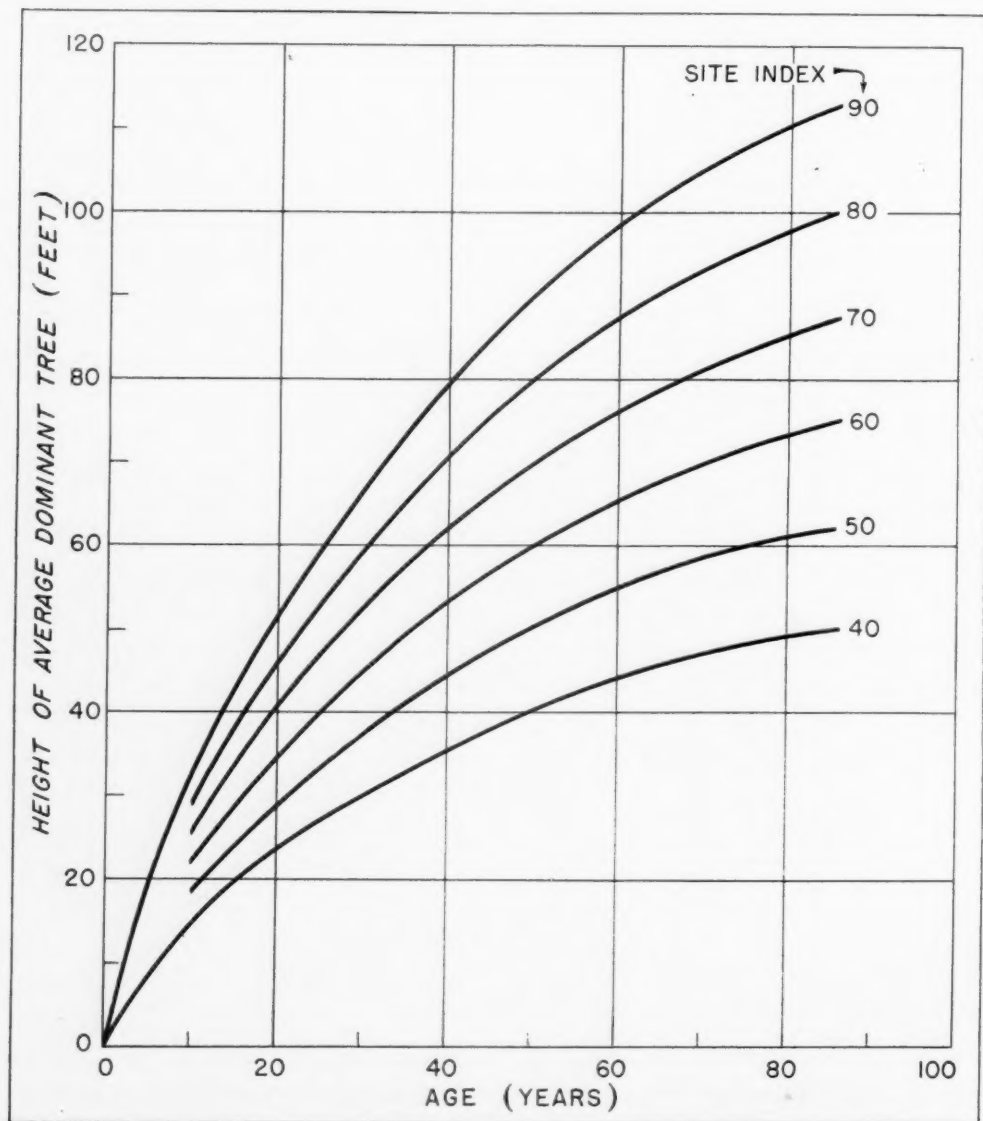
FIG. 7. Site index curves for aspen. (From Kittredge and Gevorkiantz 1929).

index graph in that average dominant height replaces volume and the relationship between height and age is represented by a curve better than by a straight line. The site indices for each plot—in reality dominant height indices—were obtained from these curves, thus providing a second measure of the habitats based on the growth of aspen.

COMPARISON OF VOLUME INDEX AND SITE INDEX

Something may be learned about these two series of measures by studying their variability. For the volume index series, the standard deviation of the 151 plots may be computed from the relation, $\sigma = \sqrt{\dfrac{\Sigma I^2 - M_I^2}{N}} = 669.4$

when $N = 151$ and the mean, $M_I = 3{,}394$. If now, the standard deviation is expressed as a percentage of the mean, a measure of the variability within the series is obtained which is known as the coefficient of variation. In symbols, $V = \dfrac{100\sigma}{M_I} = 19.8$ percent. This may be interpreted by the statement that 68 percent of the individual volume indices of the well-stocked plots lie within a range of 19.8 percent more or less than the mean.

Similarly, for the site-index series, where $N = 230$ and the mean $M_I = 62.5$, then $\sigma = 7.75$, and the coefficient of variation $V = 12.4$ percent. In other words, 68 percent of the individual site indices based on dominant height lie within a range of 12.4 percent more or less than the mean. The site-index series includes the understocked and overstocked plots which were rejected in the volume-index series. This would tend to increase the variability of the site-index series, and yet in spite of this tendency, the coefficient of variation is only 63 percent as large as that of the volume-index series. The comparison of the two series of measures indicates that the site-index is distinctly less variable than the volume-index. Partly for this reason and partly because the site index is less subject to the disturbing influence of variations in density and can, therefore, be used for all the plots including understocked and over-stocked, it will be used as the standard measure in relating aspen growth to habitat and plant-indicator groups. A further comparison of the two growth measures will be made in the correlations with soil groups.

ANALYSIS OF HABITATS

Beause the climate of the region and the local atmospheric variations within a single community are relatively uniform, and because such climatic differences as may exist are reflected in the soil, the habitat classifications are based upon the soils. Five different groupings of soils are made on the following bases: (1) Soil class or texture; (2) geological surface formation; (3) combination of soil class and surface formation; (4) soil profiles; and (5) soil types. A differentiation between the red and gray drift is made in the first three groupings. The groups will be discussed in the order enumerated above.

SOIL CLASS OR TEXTURE GROUPS

The habitat data were first classified into eight soil classes. Beginning with the coarsest, these classes are defined in terms of the component soil separates as follows:

Sand, more than 20 percent medium sand or coarser, less than 20 percent silt plus clay.

Fine sand, less than 20 percent medium sand or coarser, less than 20 percent silt plus clay.

Sandy loam, more than 20 percent medium sand or coarser, between 20 and 50 percent silt and clay.

Fine sandy loam, less than 20 percent medium sand or coarser, between 20 and 50 percent silt and clay.

Loam, less than 55 percent silt, more than 50 percent silt and clay.

Silt loam, more than 55 percent silt, less than 25 percent clay.

Clay loam and clay, less than 55 percent silt, more than 60 percent silt plus clay.

Peat, more than 50 percent organic matter.

Directly or indirectly the texture of soils affects to an important extent their complex relationships to plants. The proportions of the different separates and particularly of the finer fractions, the silt and clay and its included colloids, largely determine the water relations, the aeration, the chemical transformations and the abundance and activity of the soil organisms. In respect to the aspen community in this region, the circulation and availability of soil moisture and its reciprocal relation to aeration give a large part of their significance to the soil classes. The range of moisture contents of the different classes at the moisture equivalent (probably not far from the optimum for plants) and at the echard or wilting coefficient below which the moisture is nonavailable for growth, are shown below in tabular form. The moisture equivalents were compiled from Briggs and Shantz (1912), Middleton (1920), and others, and were converted to wilting coefficients by multiplying by the factor 0.54 as suggested by Briggs and Shantz and modified by Alway (1916) (table 4).

TABLE 4. WILTING COEFFICIENTS FOR SOIL CLASSES AS DERIVED FROM MOISTURE EQUIVALENTS

Soil Class	Moisture equivalent	Wilting coefficient
Sand	2 – 7	1 – 4
Fine sand	4 – 12	2 – 7
Sandy loam	8 – 19	4 – 10
Fine sandy loam	10 – 28	5 – 15
Loam	13 – 29	7 – 16
Silt loam	18 – 33	10 – 18
Clay loam and clay	21 – 41	11 – 22

The overlapping between the moisture "constants" of different classes is at once evident and suggests that plant responses to the different classes will not always be distinct. Furthermore, although the plants of generally mesic communities like aspen more often suffer from lack of moisture in the soils of low wilting coefficient, it is actually the presence of moisture above the

echard that is available and enables them to grow. The difference between total moisture content and wilting coefficient does not necessarily vary with the wilting coefficients. In other words, a plant may wilt in a silt loam soil with 10 percent moisture when it would grow well in a sandy loam soil with only 8 percent. One of the limitations to the establishment of the aspen community is apparently associated with a texture class. The aspen is only rarely found on the dry outwash sands which represent the least moisture-retentive texture class in the region. However, this limitation is a matter only in part of the surface layer and in part also of the subsoil and glacial formation.

The soil classes are based on the texture of the upper 8 inches of soil, and in this fact sufficient reason may be found to explain some discrepancies in the correlation of soil classes with plant growth. Most of the trees and woody plants, after their juvenile stages, have root systems extending considerably deeper than 8 inches. In these lower soil layers, the presence of a layer of heavier texture or the proximity of ground water may quite reverse the expectation as to growth judged from the soil class exclusively. Obviously the growth of aspen and the floristic composition of the community will not be the same on a fine sand along the margin of a swamp as on the fine sand of the crest of a ridge. Similarly, differences in lime content or in other chemical properties, either in the surface layer or lower in the profile, may strongly differentiate soils of the same class. The influence of different combinations of these disturbing factors may be observed in the wide variations in site index of the aspen on the same soil classes and in the systematic tendency for the site indices to be higher on the gray than on the red drift (fig. 8). Notwithstanding the discrepancies just mentioned, the soil classes of an upland well-drained area of uniform geological origin, that is of glacial material of the same age, may show a high degree of correlation with the plant responses to the different habitat conditions.

CORRELATION BETWEEN TEXTURE GROUPS AND SITE INDEX

The soil classes, subdivided into red and gray drift, provide 15 groups for the determination of the correlation ratio with site index. The distribution of the plots according to site index in each of these groups arranged in sequence from the coarse to the fine textures are shown in figure 8. In table 5, they have been rearranged in ascending sequence of mean site index (MI). The correlation ratio of 0.573 is distinctly significant. The influence of the two drifts of different origin almost entirely disarranges the sequence which would be expected from texture alone as given in figure 8, or in other words, the differences in the drift within the same soil class are usually greater than the differences between successive soil classes. This suggests that texture alone may not be an adequate basis for the classification of habitats in relation to growth.
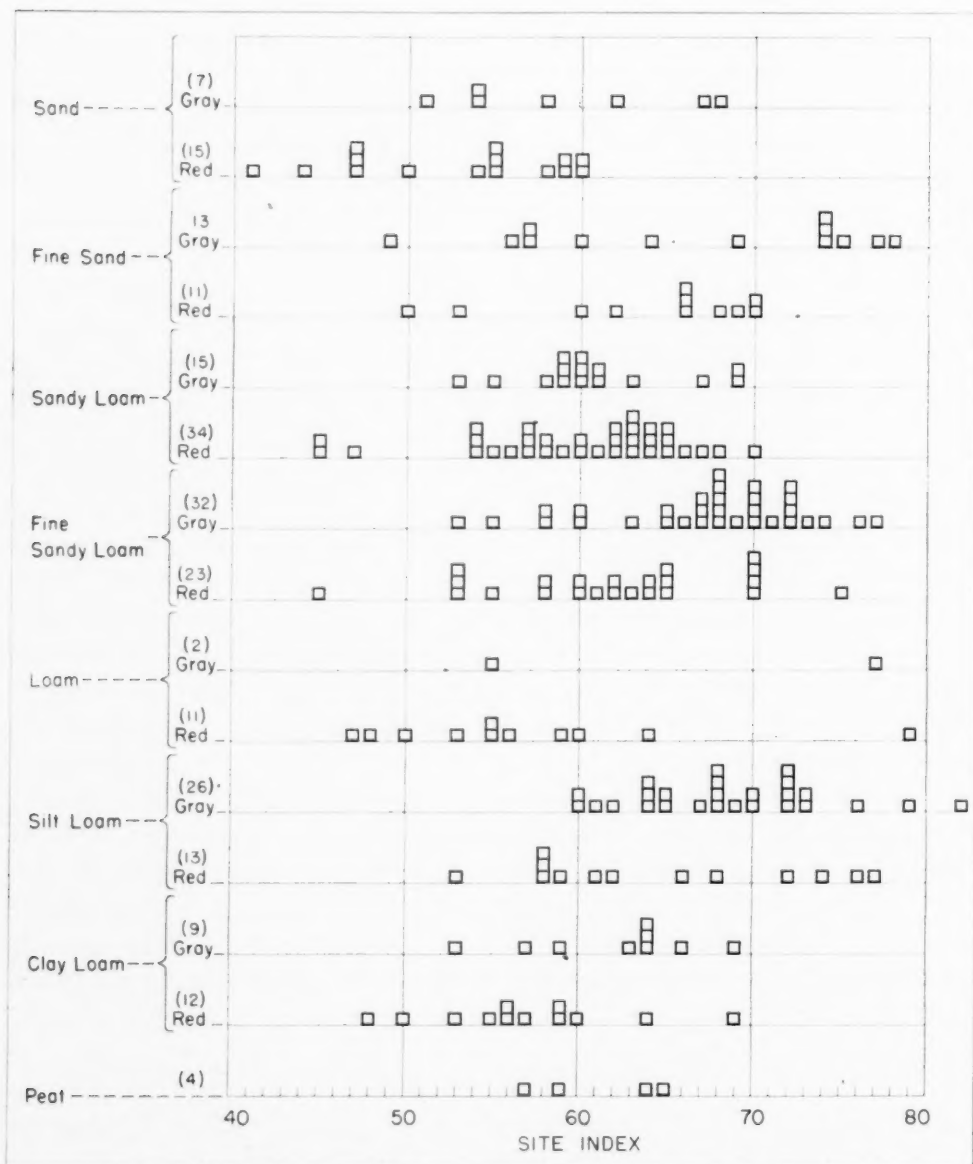
FIG. 8. Distribution of site indices by soil-texture class.

GEOLOGICAL FORMATION GROUPS

The glacial and to a minor extent other geological formations, as a basis for the classification of aspen habitats, are not wholly exclusive of texture classes. In certain groups differences in geological formation are always associated with and in fact are the cause of differences in texture classes. On the other hand, some glacial formations may be associated with several texture classes.

The nine surface formations which were distinguished were outwash, lake-bed clay, sandy moraine, rock, peat, lake-washed sandy till, lake-washed

TABLE 5. CORRELATION RATIO BETWEEN SOIL TEXTURE CLASSES AND MEAN SITE
INDEX OF ASPEN

Soil class and drift	Plots (n)	Mean site index m_I	$m_I - M_I$	$(m_I - M_I)^2$	$(m_I - M_I)^2 n$
	Number				
Sand, red drift	15	52.7	−9.8	96.0	1,440.6
Loam, red drift	11	56.9	−5.6	31.4	345.0
Clay loam, red drift	12	57.2	−5.3	28.1	337.1
Sand, gray drift	7	59.1	−3.4	11.6	80.9
Sandy loam:					
Red drift	34	59.8	−2.7	7.3	247.9
Gray drift	15	60.9	−1.6	2.6	38.4
Peat	4	61.0	−1.5	2.3	9.0
Fine sandy loam, red drift	23	61.8	−0.7	0.5	11.3
Clay loam, gray drift	9	62.1	−0.4	0.2	1.4
Fine sand, red drift	11	63.6	1.1	1.2	13.3
Silt loam, red drift	13	64.8	2.3	5.3	68.8
Loam, gray drift	2	66.0	3.5	12.3	24.5
Fine sand, gray drift	13	66.5	4.0	16.0	208.0
Fine sandy loam, gray drift	32	67.1	4.6	21.2	677.1
Silt loam, gray drift	26	68.6	6.1	37.2	967.5
$\Sigma n \ (=N)$	227				
M_I	...	62.5			
$\Sigma[(m_I - M_I)^2 n]$	...	....	.....	....	4,470.8

$$\sigma M_I = \sqrt{\frac{\Sigma[(m_I - M_I)^2 n]}{N}} = 4.44 \qquad \eta_{jt} = \frac{\sigma M_I}{\sigma_I} = 0.573$$

$$\sigma_I = 7.75$$

clayey till, clayey moraine, and till. The descriptions of these formations are familiar or are readily available in the reports of Leverett (1915) and Leverett and Sardeson (1917), for Minnesota, or in other works on glacial geology and physiography.

In their essentials for the present purpose, the outwash is a generally level deposit of deep, well-drained sand. The lake-bed clay is a deposit of clay in the beds of former lakes, level in topography and of sufficient thickness to be only slowly permeable to water and consequently having poor drainage and aeration in wet seasons. The sandy moraines are the hilly more or less assorted deposits of coarser materials, sands, and gravels, often stony. The rock formation includes the area in northeastern Minnesota where the usually igneous rocks outcrop or are within two or three feet of the surface. Peat is the postglacial accumulation of organic matter in the standing water of lakes or depressions. The lake-washed sandy till includes the sandy deposits in the shallower portions of the postglacial lakes which have been subject to wave action so that the finer materials of the original till have been removed. The lake-washed clayey till still retains much of the clayey material although it has been covered by lake waters for considerable periods. Both these deposits have level topography, and the latter in particular is apt to have deficient drainage. Clayey moraine includes the fine-textured, unassorted morainal deposits carried by and left at the retreat of the ice. Till is the unassorted

drift laid down and over-ridden by the ice, often descriptively called boulder clay.

The widely different conditions of moisture retentiveness, permeability, drainage, and aeration, and the degree to which these formations have been subjected to former water action, must evidently affect their character as plant habitats. In this respect, the first four related factors act together in differentiating the formations. Thus the formations when arranged in the following order represent increasing degrees of moisture retentiveness and decreasing degrees of permeability, drainage, and aeration: (1) Outwash, (2) sandy moraine, (3) rock, (4) till, (5) lake-washed sandy till, (6) clayey moraine, (7) lake-washed clayey till, (8) lake-bed clay, and (9) peat. Locally some differences may easily be found in the order of the middle members of the series, but in general it will hold good for these factors. The same order does not apply, however, to the amount or availability of plant nutrients, which probably reach a maximum in the till. For this and, more emphatically, for other reasons, the foregoing order does not represent an increasing or decreasing series in relation to the favorableness of the different formations as plant habitats. Evidently lack of moisture is often a limiting factor for plants on the outwash and sandy moraine and, just as truly, excessive moisture and lack of drainage become critical on the clays and on peat. The generally more favorable conditions in both respects are found near the middle of the series.

The aspen plots of each surface formation were further separated as to their location in the red or gray drift areas. The evidence of the favorable influence, presumably of the high lime content in the gray drift, will appear in figure 9, where the growth of the aspen as measured by its site index is shown for both red and gray drift of each surface formation.

CORRELATION BETWEEN GEOLOGICAL FORMATION GROUPS AND SITE INDEX

The distributions of plots according to their site indices within each formation group are shown in figure 9. In the five groups in which less than four plots occurred the red and gray drift subdivisions were combined, leaving 12 categories for the computation of correlation ratio. The essential figures are given in table 6, where they have been rearranged in ascending order of mean site index and thus do not correspond to the sequence in figure 9. In only one instance, that of the till formation, is the difference between red and gray drift greater than that between the formations themselves. Consequently, the red drift till is separated from the gray drift till by two other formations. The correlation ratio of 0.640 indicates a significant relation between the soil formations and the site indices of the aspen stands. This is a rather high degree of correlation when it is considered that soils of very different textures are grouped together in the individual formations.

If figure 9 is examined more closely, the outwash stands by itself in
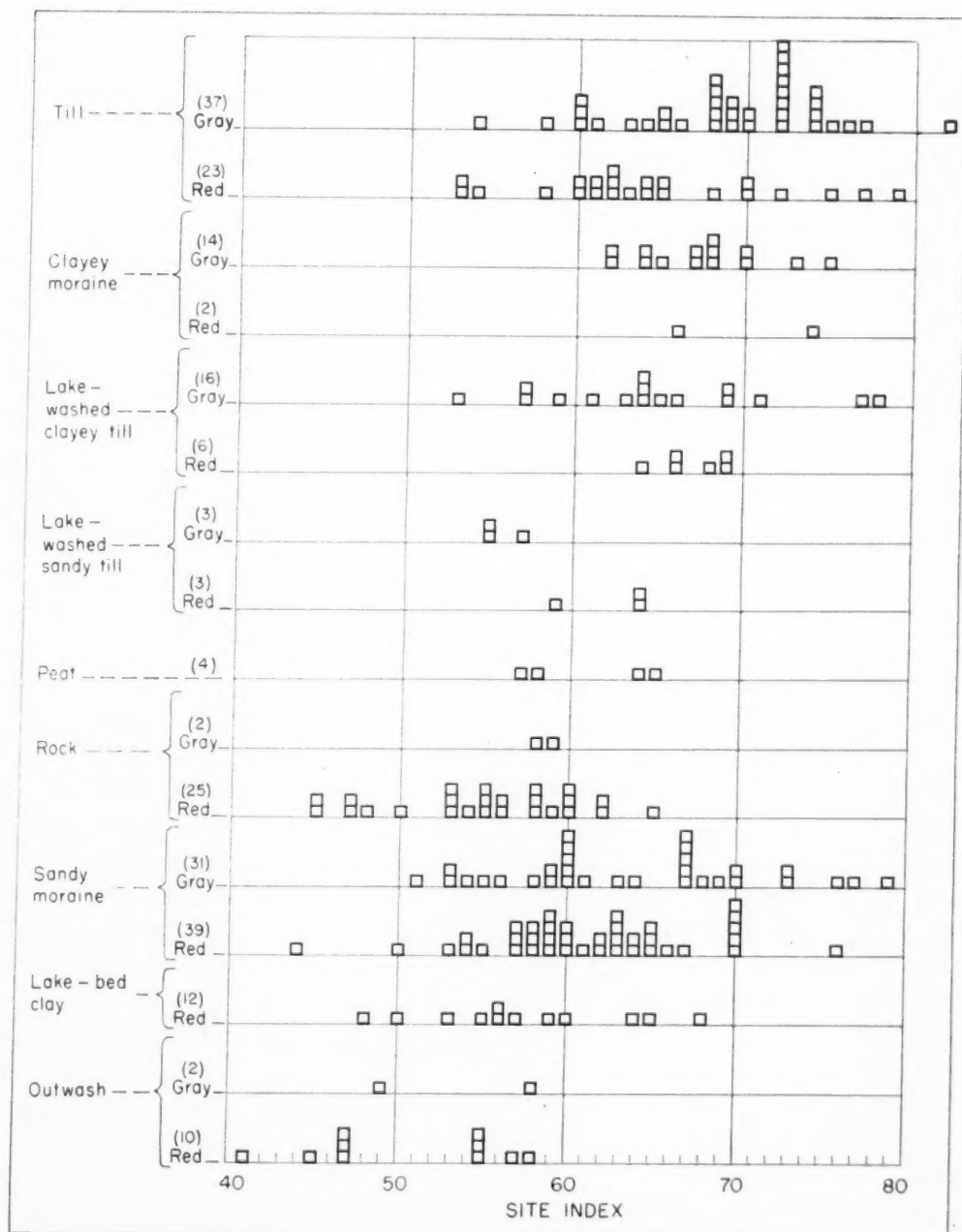
FIG. 9. Distribution of site indices by surface formation.

representing the poorest habitat for the growth of aspen. The rock and lake-
bed clay are not very different and could be considered to form a group of
somewhat less poor habitats. Sandy moraine, lake-washed sandy till, and
peat take an intermediate place in the scale of productivity. Finally, the lake-
washed clayey till, clayey moraine, and till are somewhat similar in site index
and represent the favorable surface formations for the growth of aspen. It

TABLE 6. CORRELATION RATIO BETWEEN SURFACE FORMATIONS AND MEAN
SITE INDEX OF ASPEN

Surface formation and drift	Plots (n)	Mean site index M_I	$m_I - M_I$	$(m_I - M_I)^2$	$(m_I - M_I)^2 n$
	Number				
Outwash, red and gray drift...............	12	51.2	−11.3	127.7	1,532.3
Rock, red and gray drift.......ᵥ...........	27	55.2	− 7.3	53.3	1,438.8
Lake-bed clay, red drift...................	12	57.6	− 4.9	24.0	288.1
Lake-washed sandy till, red and gray drift...	6	59.0	− 3.5	12.3	73.5
Peat, red and gray drift..................	4	61.0	− 1.5	2.3	9.0
Sandy moraine:					
Red drift...........................	39	61.3	− 1.2	1.4	56.2
Gray drift..........................	31	63.7	1.2	1.4	44.6
Till, red drift...........................	23	64.3	1.8	3.2	74.5
Lake-washed clayey till:					
Gray drift..........................	16	64.8	2.3	5.3	84.6
Red drift...........................	6	67.0	4.5	20.3	121.5
Clayey moraine, red and gray drift........	16	67.7	5.2	27.0	432.6
Till, gray drift..........................	37	68.8	6.3	39.7	1,468.5
$\Sigma n \ (=N)$.........................	229				
M_I................................	...	62.5			
$\Sigma[(m_I - M_I)^2 n]$.................	...	....	....	....	5,624.4

$$^{\sigma}M_I = \sqrt{\frac{\Sigma[(m_I - M_I)^2 n]}{N}} = 4.96 \qquad\qquad n_{it} = \frac{^{\sigma}M_I}{\sigma_I} = 0.640$$

$$\sigma_I = 7.75$$

may be noted that this is not the order of moisture and aeration relations
previously discussed. The outwash with deficient moisture and the lake-bed
clay with seasonally excessive moisture and lack of aeration stand close
together as unfavorable habitats as measured by the growth of aspen. The
favorable habitats are the lake-washed clayey till, clayey moraine, and till—
formations with neither deficient nor excessive moisture, or at worst those
of the latter class with reasonably good drainage.

As compared with the texture classes on the basis of the aspen site indices,
the surface formations are the more closely correlated with site index, as
indicated by the correlation ratio of 0.64 as compared with 0.57 for the
texture classes. In other words, if it were necessary to choose between the
surface formations and texture classes as a basis for the classification of soil
productivity for tree growth, the surface formations would give the better
correlation. The two forms of classification are obviously not mutually ex-
clusive and are in many respects closely related, but, as a whole, the surface
formations seem to integrate more completely the growth factors which
influence aspen than do the texture classes.

COMBINED TEXTURE AND GEOLOGICAL-FORMATION GROUPS

If now the two preceding groupings are combined into a single series, it
should be possible to find a classification on this basis which would be more
closely correlated with aspen growth than were either of the foregoing series
alone. This was done, by subdividing the surface formations into texture

classes and further modifying the groups thus formed by the fact already established that the gray drift as compared with the red drift caused as much difference in habitat factors as that between two adjacent soil classes. In order to avoid having more groups than could be satisfactorily treated biometrically with the data available, some of them were recombined, so that finally the following 12 groups were differentiated: On the outwash, the sands and fine sands formed one group and the sandy loam or heavier textured soils a second. On rock, one group comprised fine sands, sandy loams and loams, and a second, fine sandy loams and silt loams. Clay loam and clay on lake-bed clay formed a fifth group. The sandy moraine and lake-washed sandy till were combined for the coarser-textured classes into a group for the sands and a second for the red-drift fine sands and sandy loams. Gray-drift sandy loams on lake-washed sandy till were combined with fine sandy loams and heavier-textured soils on this and on the sandy-moraine formation. In other words, a sandy loam on the gray drift was considered to be more nearly equivalent to a fine sandy loam or loam on the red drift than to a soil of the same class on that drift. Peat was retained as a distinct group as was clay loam on lake-washed clayey till. Gray-drift sands and fine sands and red-drift sandy loams and fine sandy loams on till, clayey moraine, and lake-washed clayey till were all combined into one group. For the same three formations, the gray-drift sandy loams and fine sandy loams were grouped with the red-drift soils of textures finer than fine sandy loam, making the twelfth group.

In this grouping, the same growth factors are involved that have been discussed for the separate soil classes and surface formations, but the foregoing arrangement combines them in groups in which they reinforce and intensify one another instead of conflicting and nullifying, as was the case in the earlier classifications. For example, the sandy-texture class in combination with the outwash formation makes a more distinct group than could be had if several texture classes were included in the outwash group or if two or more surface formations were combined in a class of sands. This grouping of combinations of soil classes and geological formations is in effect a soil classification in broad categories based only on texture class and geological origin, but it serves to combine in rather distinct and homogeneous groups the more important edaphic factors which influence plant growth.

CORRELATION WITH SITE INDEX AND DIFFERENTIATION OF COMBINED TEXTURE AND GEOLOGICAL-FORMATION GROUPS

These 12 groups and the basis for the calculation of correlation ratio with site index are arranged in table 7 in ascending order of mean site index. The distributions of plots in each group are shown in figure 10, where the group numbers correspond to those at the extreme left in table 7. This ratio of 0.699 represents a decidedly higher degree of correlation than was obtained with either of the previous groupings. The conclusion seems justified that a

TABLE 7. CORRELATION RATIO BETWEEN COMBINED TEXTURE-SURFACE FORMATION
GROUPS AND MEAN SITE INDEX OF ASPEN

Soil group	Plots (n)	Mean site index m_I	$m_I - M_I$	$(m_I - M_I)^2$	$(m_I - M_I)^2 n$
	Number				
1. Sands and fine sands on red-drift outwash.	7	48.7	−13.8	190.4	1,333.1
2. Sandy loam and heavier on red-drift out-wash	4	53.7	− 8.8	77.4	309.8
4. Clay loam on lake-bed clay	9	54.9	− 7.6	57.8	519.8
5. Red-drift fine sandy loam and silt loam on rock	8	55.1	− 7.4	54.8	438.1
3. Red-drift fine sand, sandy loam, and loam on rock	19	55.3	− 7.2	51.8	985.0
6. Sands on sandy moraine and on lake-washed sandy till	13	55.3	− 7.2	51.8	673.9
8. Peat	4	61.0	− 1.5	2.3	9.4
7. Red-drift fine sand and sandy loam on sandy moraine and lake-washed sandy till.	23	61.4	− 1.1	1.2	27.8
9. Clay loam on lake-washed clayey till	12	62.6	0.1	0.01	0.1
11. Sandy loam on gray drift; and fine sandy loam and heavier on sandy moraine or lake-washed sandy till	39	64.6	2.1	4.4	176.4
10. Sand and fine sand on gray drift; sandy loam, and fine sandy loam on red drift, on till, clayey moraine, or lake-washed clayey till	34	64.9	2.4	5.8	195.8
12. Sandy loam and fine sandy loam on gray drift; and heavier red-drift soils on till, clayey moraine, or lake-washed till	58	68.5	6.0	36.0	2,088.0
$\Sigma n (= N)$	230				
M_I	...	62.5			
$\Sigma [(m_I - M_I)^2 n]$	...	....	......	....	6,757.2

$$^\sigma M_I = \sqrt{[\Sigma (m_I - M_I)^2 n]} = 5.42 \qquad \eta_{JI} = \frac{^\sigma M_I}{^\sigma_I} = 0.699$$

$$^\sigma_I = 7.75$$

combination of soil texture classes and surface formations affords a classification of the habitats of the aspen community more closely related to their productivity as measured by site index than do either soil classes or surface formations alone.

Some interesting suggestions in regard to the influence of different edaphic factors on the growth of aspen may be derived from the order in which the groups are arranged according to their mean site indices in table 7. The fact that the outwash sands, on which the aspen community is rarely found, have the lowest productivity—even the heavier textured soils on this formation being lower on the average than those of any other group—and that they have the lowest moisture-retaining capacity and are also lowest in nutrient contents of any of the groups suggests that they are close to representing limiting edaphic conditions for the species.

Next above the outwash in the site-index scale come the clay and clay loams on lake-bed clay, a group with strikingly different properties. They are chiefly the red clays of the bed of Lake Duluth, the finest textured and
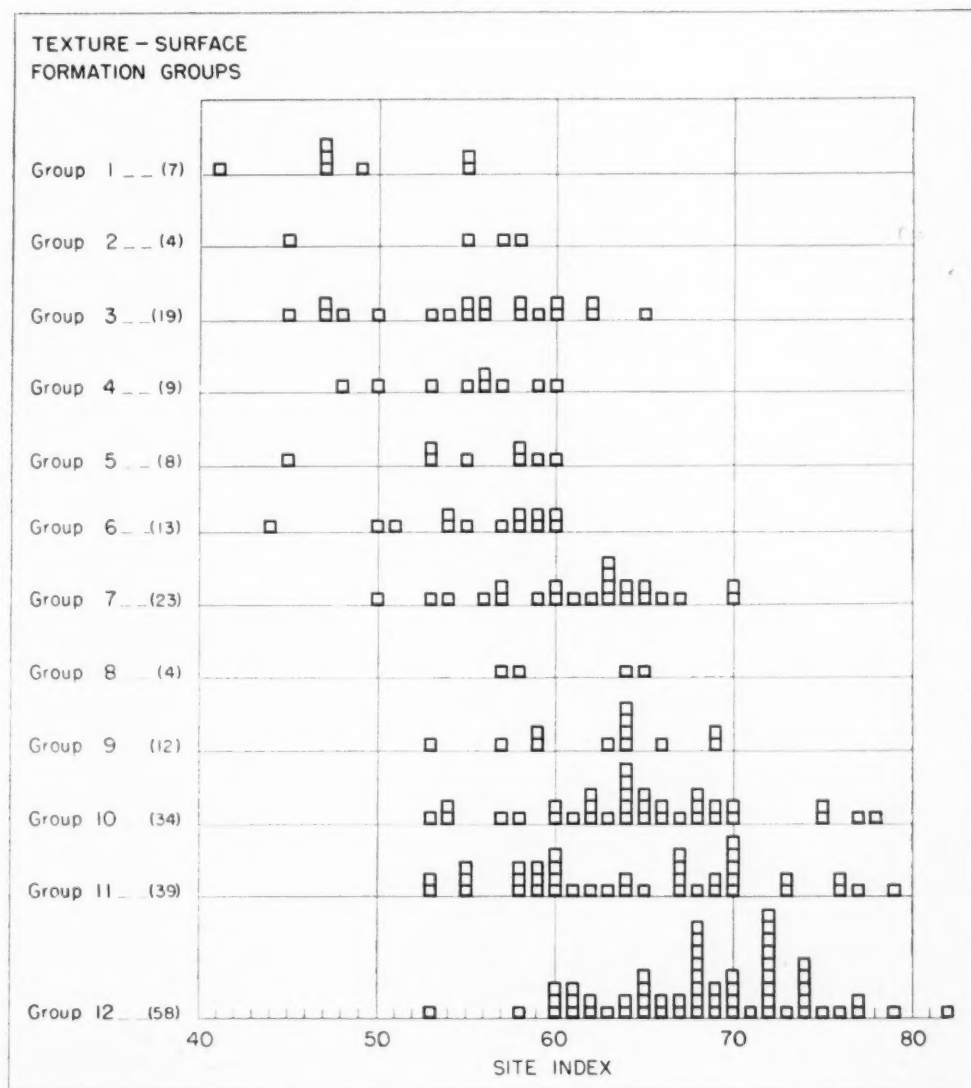
FIG. 10. Distribution of site indices by combined soil-texture and surface-formation groups.

most moisture-retentive mineral soils in the region, so much so that drainage is often poor and aeration deficient. The slow growth on this group is evidently caused by a set of factors quite different from those that were operative in the outwash groups, yet the net result as expressed in the growth of aspen is closely similar. The soils of the rock formation and the sands of the sandy moraine and lake-washed sandy till are only slightly higher than the clays. These groups, like the outwash, represent habitats not far removed from a xeric origin. Above them comes the group of fine sands and sandy loams on sandy moraine or lake-washed sandy till of the red drift, more favorable in moisture and fertility because of their finer texture. Close to this

group come the hydric peat and clay loam on lake-washed clayey till, which
tend to resemble the lake-bed clay in properties and to contrast with the
preceding xeric groups.

The two large mesic groups—the gray-drift sand and fine sand and red-
drift sandy loam and fine sandy loam on till, clayey moraine, and lake-washed
clayey till and the gray-drift sandy loam and fine sandy loam and heavier soils
on sandy moraine or lake-washed sandy till—are · respectively the lighter
texture classes on the less permeable formations and the heavier texture
classes on the more permeable formations, an example in their ·identity of site
index, of the reciprocal effect of surface texture and underlying glacial
deposit.

Finally the most favorable habitats as measured by aspen growth are in-
cluded in the group of sandy loams and fine sandy loams of the gray drift and
the heavier red-drift soils on till, clayey moraine, or lake-washed till. This is
the group of mesic or slightly hydro-mesic formations with mesic surface-soil
layers, which might be expected to favor the development of aspen or of any
other mesic community.

Are these 12 groups distinct, considering the variability and overlapping
of the site-index values of the individual plots? The difference between the
means of any two groups may be tested biometrically by computing the stand-
ard deviation of their difference. Using this measure as modified for small
numbers by Fisher (1930) in what he calls the "t" test for the significance
of a difference between two means, "t" is calculated (for large numbers of
observations it is simply the ratio between the difference of the two means
and the standard deviation of that difference) and, from its value and that of
"n," the number of degrees of freedom in the two series, the probability that
the difference may be due to chance. An example will make clear the method
of calculation and the interpretation. In the first two groups in figure 10,
there are 7 and 4 site-index values respectively, and therefore the degrees of
freedom are $n_1 = 6$ and $n_2 = 3$. The corresponding mean values of site
index are $MI_1 = 48.7$ and $MI_2 = 53.7$, and $MI_2 - MI_1 = 5.0$. $n = n_1$
$+ n_2 = 6 + 3 = 9$. Then —

$$\Sigma(I_1 - MI_1)^2 = \Sigma I_1^2 - (n_1 + 1)M^2 I_1 = 16{,}759 - 7(48.7)^2 = \underline{155}$$

$$\Sigma(I_2 - MI_2)^2 = \Sigma I_2^2 - (n_2 + 1)M^2 I_1 = 11{,}663 - 4(53.7)^2 = \underline{127}$$

$$\Sigma(I_1 - MI_1)^2 + \Sigma(I_2 - MI_2)^2 = \overline{282}$$

The square of the standard deviation of the difference is—

$$\sigma^2{}_{(M_{I_2} - M_{I_1})} \left(\frac{1}{n_1 + 1} + \frac{1}{n_2 + 1} \right) = \frac{n_1 + n_2 + 2}{(n_1 + 1)(n_2 + 1)(n_1 + n_2)}$$

$$\left[\Sigma(I_1 - MI_1)^2 + \Sigma(I_2 - MI_2)^2 \right] = 12.3, \text{ and } t =$$

$$\frac{M_{I_2} - M_{I_1}}{\sigma(M_{I_2} - M_{I_1}) \sqrt{\dfrac{1}{n_1 + 1} + \dfrac{1}{n_2 + 1}}} = \frac{5.0}{\sqrt{12.3}} = 1.43.$$

Then from Fisher's table IV for this value of "t" and $n = 9$, we find $P = 0.2$, which is to say that the chances are 20 in 100 that the difference between the mean site indices of the first two soil groups may be due wholly to random errors of sampling. If a probability of 0.05 or 5 chances in 100 is accepted as the limit for deciding whether or not a difference is significant, then clearly the sands and fine sands are not significantly different from the sandy loams and heavier soils on the outwash formation. This criterion of differences is, of course, based entirely upon the variability of the site index value of the two soil groups being tested, and shows nothing except in that way as to the logic or lack of logic in the physical or biological relationships between them. Actually, in this instance the surface formation is the same in both groups while the texture classes are different, so that they have a bond of relationship and the difference between them might logically be expected to be small.

Similar tests were made as to the significance of the differences between each two groups where there seemed to be any question. A summary of the results is given below in table 8, using the numbers as given in figure 10 and table 7 to designate the different soil groups.

TABLE 8. SUMMARY OF TEST OF DIFFERENCE IN SOIL GROUPS

Soil groups	$M_{I_2} - M_{I_1}$	n_2	n_1	n	t	P	Significance of difference
2 - 1	5.0	3	6	9	1.43	0.2	—
3 - 2	1.6	18	3	21	0.53	0.6	—
4 - 1	6.2	8	6	14	2.81	0.02	+
8 - 6	5.7	3	12	15	2.12	0.05	+
10 - 8	3.9	33	3	36	1.21	0.24	—
12 - 10	3.6	57	33	90	2.43	0.02	+
I - II	4.8	57	111	168	5.0	0.01—	+
II - III	8.6	111	52	163	9.8	0.01—	+
III - IV	3.4	52	6	58	6.4	0.01—	+

From the upper section of the table it may be concluded, first, that group 2 is not significantly different from group 1, and second, that group 3 is not significantly different from 2. Group 4, however, is significantly different from group 1, and as groups 3, 5, and 6 are higher in mean site index than 3, they also may be assumed to be significantly different from 1. Group 8, the lowest of the remaining groups, is significantly different from group 6, the highest of the preceding groups. Between 6 and 8 then, is a line of division not only between those two groups but between the several which are adjacent to them or, if it were desirable, between two parts into which the whole array of plots could be divided. Finally group 12 is significantly different from 10 and also from 11 and 9, 8 and 7. On the basis of these tests, then, larger

groupings were made, each containing one or more of the original groups. Each of these groupings when tested by the same "t" test in the lower portion of the foregoing tabulation proves to be significantly different from the others.

From the practical standpoint in the determination of forest productivity or site quality for the growth of aspen, it would be highly desirable and convenient to be able to classify the aspen lands in four distinct site qualities on the basis of soil texture and surface formation. It will be interesting to see, however, if these groupings have any physical and biological homogeneity or if they must be considered as artificial categories without such unity. For the moment these combined groups may be called site qualities. Then site quality I includes only group 12, consisting of sandy loams and fine sandy loams of the gray drift and the heavier red-drift soils on till, clayey moraine, or on lake-washed till, and can be considered a homogeneous natural unit. Site quality II includes groups 7, 8, 9, 10, and 11. Among these appear such diverse groups as peat and clay loam on lake-washed clayey till on the hydric side and fine sand and sandy loam on sandy moraine on the xeric side. This site quality obviously cannot be considered to be made up of a grouping of unified natural habitats. It happens to be quite uniform in respect to the growth of aspen but this uniformity is the resultant of the combined effects of very different combinations of factors. Site quality III includes groups 3, 4, 5, and 6 and because 2 has been shown to be much nearer 3 than 1, it is also included.

Here again the component groups make a heterogeneous combination. On the xeric side are the sandy loams on outwash and the sands on sandy moraine, and on the hydric, the clay loams and clays on lake-bed clay. Furthermore, the two groups on the rock formation are also included which are quite different from either of the foregoing groups. As in site quality II, this grouping also has no natural homogeneity except as to the growth of aspen. Site quality I comprises only the one group of sands and fine sands on outwash and is therefore a natural unit. It would, of course, be possible to separate site qualities II and III into their xeric and hydric components and thereby establish a somewhat larger number of categories (but still less than 12). These would have some biological homogeneity but would only in part be distinguishable by the site index of the aspen. Thus far the conclusion is suggested that the growth rate of aspen will serve to differentiate the habitats into four rather broad categories which cannot be considered to have natural homogeneity.

The relationship between the 12 groups based on soil texture and geological formation may also be tested by another biometrical device. Pearson (1906-7) has suggested a method of determining the significance of the difference between a subsample and the whole sample of which it forms a part. By this method the significance of the difference between the mean site

index for each group and that of the whole sample of 230 plots was computed. Algebraically the function may be represented by the expression—

$$\frac{m_I - M_I}{\sqrt{\dfrac{\sigma_n^2}{n} - \dfrac{2\sigma_n^2 - \sigma_N^2}{N} - \dfrac{n(M_I - m_I)^2}{N(N - n)}}}$$

This is in effect the ratio of the actual difference between the means of sub-sample and sample divided by the standard deviation of the difference of those means corrected for the influence of the relationship between sample and subsample. The foregoing formula makes no allowance for small numbers of cases, hence the values for those groups with only a few plots may not be wholly reliable. The essentials of the computation and the results are shown in table 9. The statistical constants for the whole 230 plots, are $N = 230$,

TABLE 9. THE SIGNIFICANCE OF THE DIFFERENCE BETWEEN THE MEAN SITE INDEX OF EACH GROUP AS A SUBSAMPLE AND ALL OF THE PLOTS AS A SAMPLE

Soil group	$m_I - M_I$	n	$\dfrac{\sigma_n^2}{n}$	$\dfrac{2\sigma_n^2 - \sigma_N^2}{N}$	$\dfrac{n(M_I - m_I)^2}{N(N-n)}$	c	$\dfrac{m_I - M_I}{\sqrt{c}}$
1	−13.8	7	3.20	+0.07	−0.03	3.24	−7.6
2	− 8.8	4	8.02	− .02	− .01	7.99	−3.1
3	− 7.2	19	1.4	+ .03	− .02	1.5	−6.0
4	− 7.6	9	1.4	+ .15	− .01	1.54	−6.1
5	− 7.4	8	3.0	+ .06	− .01	3.05	−4.2
6	− 7.2	13	1.6	+ .08	− .01	1.67	−5.6
7	− 1.1	23	1.1	+ .05	.00	1.15	−1.0
8	− 1.5	4	3.1	+ .15	.00	3.25	−0.8
9	+ 0.1	12	1.5	+ .10	.00	1.60	+0.1
10	+ 2.4	34	1.1	− .07	.00	1.03	+1.9
11	+ 2.1	39	1.2	− .14	.00	1.06	+2.0
12	+ 6.0	58	0.6	− .03	− .05	0.52	+8.3

$M_I = 62.5$ and $\sigma_N^2 = 60.06$. For convenience the long expression under the radical in the denominator of the formula will be designated by "c". "m_I" is the mean site index for a group, and "n" is the number of plots in a group. The standard deviation of a group is designated σ_n.

The fact that the values of the ratio in the last column form a progressive series, increasing from − 7.6 to 0 and on up to + 8.3, is in itself a demonstration that the groups have a systematic arrangement and progression of the mean site-index values. The two erratic values for groups 2 and 5 are doubtless caused by the small number of cases and consequently abnormal distributions from which the biometric constants had to be calculated. The same four groupings or site qualities which were indicated by the significant differences between groups may also be distinguished by this method. Group 1 with a ratio of − 7.6 stands by itself. Groups 2, 3, 4, 5, and 6 with ratios from −6.1 to − 3.1 (probably low) may logically be combined. Groups 7, 8, 9, 10, and 11 with values from − 1.0 to 2.0 form a third grouping, and group

12 with a ratio of 8.3 makes the fourth. The two methods therefore confirm one another, in showing that the site-index values of aspen serve to differentiate broad groupings of habitats, but, as previously pointed out, these groupings are not physically and biologically homogeneous.

CORRELATION BETWEEN COMBINED TEXTURE AND GEOLOGICAL FORMATION GROUPS AND VOLUME INDEX

For the same 12 habitat groups, the mean-volume indices were determined from the distributions of the individual plot-volume indices of the 151 well-stocked plots. The distributions are shown in figure 11. The wide dispersion
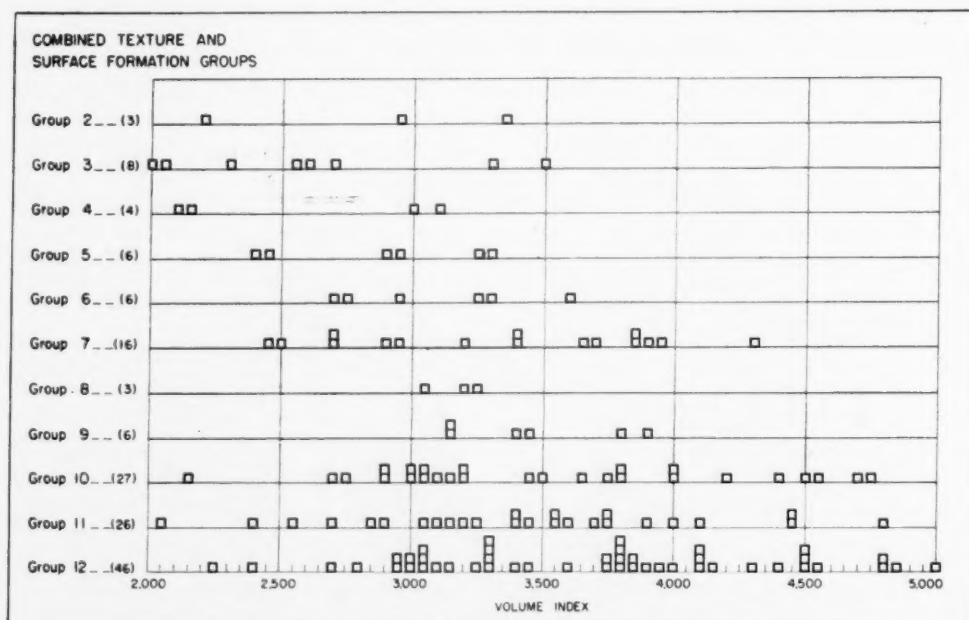
FIG. 11. Distribution of volume indices by combined soil-texture and surface-formation groups.

of volume indices in almost all of the soil groups is noticeable. Group 1 did not have any well-stocked plots and therefore is not represented. The essential figures for the computation of the correlation ratio between mean volume index and the texture-surface formation groups are shown in table 10. The soil groups are arranged in ascending order of mean volume index. The numbers in parentheses are those of the soil groups as they have been used in the foregoing discussions. Some changes in order have been made as a result of using volume index instead of site index, but the changes are in those groups which are closely adjacent and in which no significant difference between the means could be shown.

The correlation ratio between the soil texture-surface formation groups and volume index of 0.46 may be compared with the corresponding figure of 0.70 obtained in the correlation of the same soil groups with site index. The

TABLE 10. CORRELATION RATIO BETWEEN SURFACE FORMATION-TEXTURE GROUPS AND VOLUME INDEX

Soil group	Plots (n)	Mean volume index m_I	$m_I - M_I$	$(m_I - M_I)^2$	$(m_I - M_I)^2 n$
	Number				
Sands and fine sands on red drift outwash (1).	0	.....	...	....	....
Clay loam on lake-bed clay (4).............	4	2,593	801	641,601	2,566,404
Red drift fine sand, sandy loam and loam on rock (3)...........................	8	2,619	775	600,625	4,805,000
Sandy loam and heavier on red drift outwash (2)...........................	3	2,837	557	310,249	930,747
Red drift fine sandy loam and silt loam on rock (5)...........................	6	2,870	524	274,576	1,227,456
Sands on sandy moraine and on lake-washed sandy till (6).......................	6	3,090	304	92,416	554,496
Peat (8).................................	3	3,160	234	54,756	164,268
Red drift fine sand and sandy loam on sandy moraine and on lake-washed sandy till(7)	16	3,335	59	3,481	55,696
Sandy loam on gray drift and fine sandy loam and heavier on sandy moraine or on lake-washed sandy till (11)................	26	3,426	32	1,024	16,384
Clay loam on lake-washed clayey till (9).....	6	3,467	73	5,329	31,974
Sand and fine sand on gray drift, sandy loam and fine sandy loam on red drift, on till, clayey moraine or lake-washed clayey till (10).............................	27	3,529	135	18,225	492,075
Sandy loam and fine sandy loam on gray drift and heavier red drift soils on till, clayey moraine or on lake-washed till (12).....	46	3,670	276	76,176	3,504,096
$\Sigma n (= N)$..........................	151				
M_I..................................	...	3,394			
$\Sigma[(m_I - M_I)^2 n]$....................	...	.....	...		14,348,596

$$\sigma M_I = \sqrt{\frac{\Sigma(m_I - M_I)^2 n}{N}} = 308.3 \qquad \tau_{It} = \frac{\sigma M_I}{\sigma_I} = 0.461$$

$$\sigma_I = 669.4$$

considerable difference is probably caused in large part by the wider dispersion of the individual volume-index values within groups and in the whole array than of the site-index values. This was anticipated in a previous section where the coefficients of variation were found to be 19.8 percent for the volume-index series and 12.4 percent for the site-index series. Moreover, the advantage in favor of the site index holds notwithstanding the fact that the volume-index data are limited to the well-stocked plots, a more homogeneous group, at least with respect to variations in density. The conclusion seems to be substantiated that site index is a more reliable and more distinctive criterion of aspen growth as a measure of the productivity of habitats than is stem volume growth.

SOIL PROFILE GROUPS

The soil profile, as an integrated expression of all the factors of the local environment which have had time to express themselves, should theoretically give a closer correlation with plant growth than the previously discussed soil groups which have been based on only a part of the habitat factors. The soil

types described in the more recent soil surveys have uniform profiles within rather narrow limits of variation.

SOIL TYPES AS PROFILE UNITS

At least the variation in the profile within any soil type is less than the differences which exist between soil types. The soil type will therefore be considered to represent a profile unit and the smallest habitat unit which will be considered. Any difference in the texture, geological formation, ground water, or chemical and biological activity, including the influence of the higher vegetation, will be reflected in the profiles and in a differentiation of soil types if the soil-forming processes have been sufficiently prolonged or intense.

The 277 plots of the aspen community represent 54 different soil types, and probably the number would be a little larger if detailed soil surveys had been available for all the areas from which the samples were taken. This seems like a large number of habitats on which to find a community dominated by the same species, but it is quite certain that if the study had been extended to eastern Wisconsin and adjacent Michigan the number would have been more than doubled. In the absence of soil surveys, local geographic names were given to soil types which were evidently distinct from any that had been described. The list of types and the distribution of site indices of the aspen plots on each of them, arranged in 22 groups in ascending order of median site index, are shown in figure 12.

Again the variation of site index within the same soil type and the overlapping of the distributions of adjacent types is evident, as it has been in each of the foregoing coarser classifications. The finer subdivisions of the material into something approaching the smallest units of habitat which could be conveniently distinguished as representing a community does not eliminate the variability which results in part from variations within a single soil type and in part from biological variations in the aspen species and individuals. This degree of refinement in classification has already caused the distribution of the plots in so many classes that biometrical measures would be almost meaningless for most of the classes. Further subdivision would only increase the difficulty. The suggestion of most interest to be derived from these considerations is that no single or average measure of the growth of trees or vegetation is specifically applicable to any other habitat than the particular one in which the trees are growing and no attainable refinement of classification is likely to make it applicable. With the amount of material available, therefore, it becomes necessary to devise a classification of soil profiles into less numerous categories than are afforded by the soil types.

SCHEME OF GROUPING BASED ON PROFILE FEATURES

The soil profile descriptions offer a wealth of material upon which to base a classification. Each of the four or more horizons is characterized as to
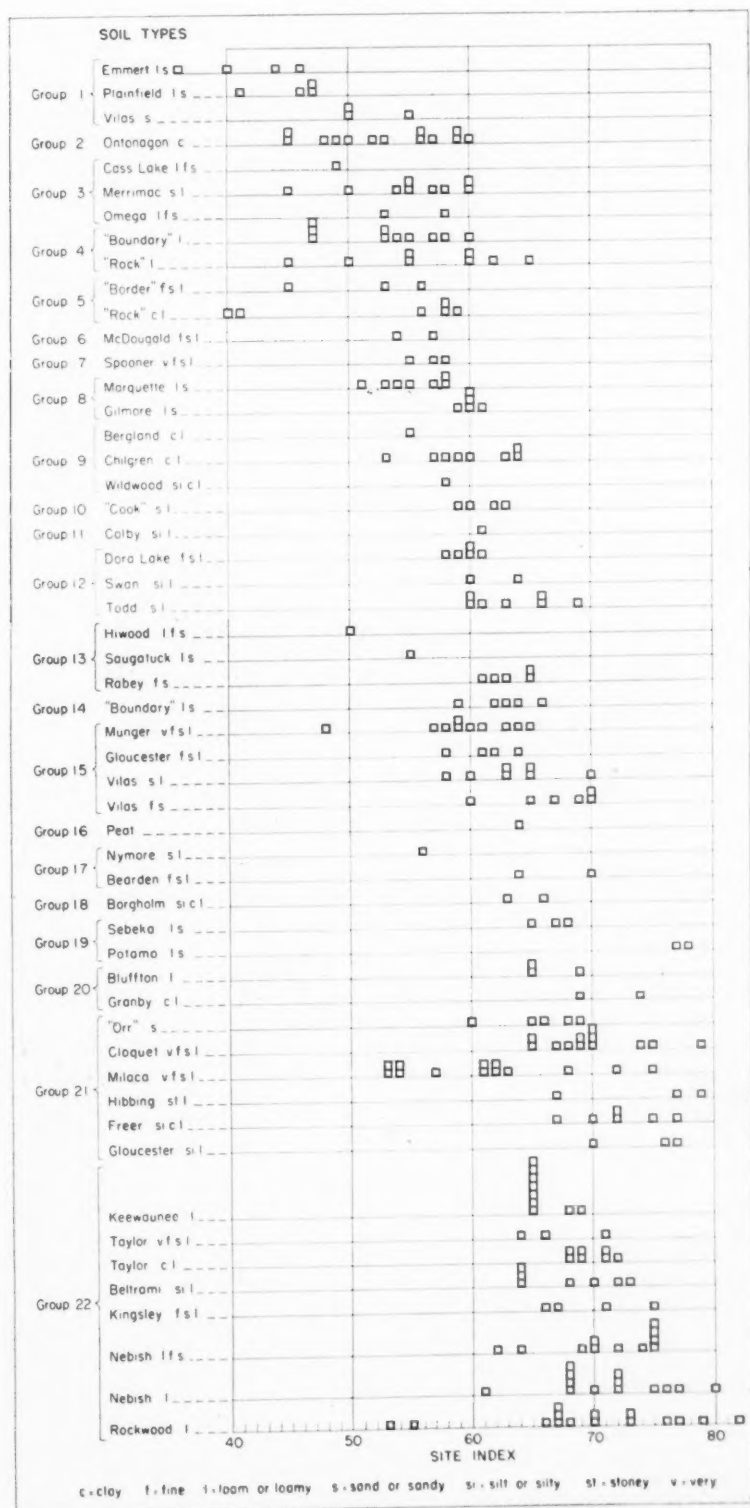
FIG. 12. Distribution of 277 aspen plots, by site index, in 54 different soil types, classified in 22 groups.

thickness, texture, color, consistency, and certain easily determined chemical
and biological particulars. Fortunately certain combinations of these features
are associated; in those cases it is only necessary to decide which are most
significant and convenient. The different horizons of the profiles will be
designated by the Russian system of letters and subscripts, which is probably
in more general use in the United States than any other one system.

The A_0 horizon of organic matter at the surface has few distinguishing
characteristics within a relatively uniform community like the aspen, except
in situations of excessive moisture where it becomes abnormally thick with
the formation of peat. The A_1 horizon includes the upper layer of mineral
soil, which is dark-colored owing to its high content of organic matter. This
layer is ordinarily thin in the podsolic soils but becomes distinctively thick in
some of the swamp-margin soils. The A_2 horizon of eluviation varies
markedly with changes in environmental influences and hence is useful for
classification. Strong development of the A_2 is indicated by the light gray
color and the degree of contrast and sharpness of the transition to the under-
lying horizon. Poor development, on the contrary, lacks these distinctive fea-
tures. The horizon is thin and often grades imperceptibly into the underly-
ing B horizon. In this region the soils with poorly developed A_2 horizon are
associated with certain of the xeric and hydric habitats, whereas those with a
strong A_2 are in the mesic group.

The intensity of development of the B horizon of illuviation is closely
related to the A_2 horizon, that is, strong development of the A_2 is associated
with strong development of the B, with certain exceptions to be noted. For
the present purpose the characteristics of the B horizon seem to offer little
that is not as well distinguished by the A_2 horizon, and therefore the B does
not appear in the following categories of classification. The notable exception
of which use has been made is the occurrence of a G or glei horizon in place
of the B horizon in those soils which have developed under the influence of
a high water table. The glei horizon is characteristically grayish or greenish
with streaks and mottlings of yellow, orange, and rust brown. The C horizon
of unweathered parent material underlying the solum is important chiefly in
respect to its texture, water-holding capacity, and lime content. These fea-
tures are made the basis for division of the C horizon into sandy, clayey, and
rock. Subdivisions of each are designated as calcareous and noncalcareous.
The soils with clayey calcareous C horizon were further separated into two
classes—well-drained and poorly drained. In certain groups the sands are
separated from the heavier soils.

The resulting classification of soil profiles and the soil types which belong
in each of the 22 categories are shown in table 11. This serves not only to
group the soil types but also to characterize them as to their profile char-
acteristics and indicate those which are related. The degree of relationship is

TABLE 11. CLASSIFICATION OF SOIL PROFILES[1]

Character of C horizon	XERIC Weak A2 horizon		MESIC Strong A2 horizon		HYDRIC Weak A2 horizon	
	Sands	Heavier soils	Without glei horizon	With glei horizon	Ao thin, A1 thick	Ao thick, A1 thin
Sandy Noncalcareous	GROUP 1— Emmert l.s. Plainfield l.f.s. Vilas s.	GROUP 3— Merrimac s.l. Omega l.f.s. Cass Lake l.f.s.	GROUP 15— Gloucester f.s.l. Vilas sandy l.&f.s. Munger v.f. s.l.	GROUP 13— Saugatuck l.s. Hiwood l.f.s. Rabey f.s.		GROUP 16— Peat
Calcareous	GROUP 18— Marquette l.s. Gilmore l.s.	GROUP 17— Nymore s.l. Bearden f.s.l.	GROUP 12— Dora Lake f.s.l. Swan si.l. Todd s.l.	GROUP 19— Sebeka l.s. Potamo l.s.	GROUP 20— Bluffton l. Granby c.l.	
Rock Noncalcareous	GROUP 14— "Boundary" l.s.	GROUP 4— "Rock" l. "Boundary" l.	GROUP 5— "Rock" c.l. "Border" f.s.l.			
Clayey Noncalcareous		GROUP 10— "Cook" s.l.	GROUP 21— "Orr" s. Cloquet v.f.s.l. Milaca v.f.s.l. Hibbing st.l. Gloucester si.l. Freer si. c.l.	GROUP 11— Colby si.l.	GROUP 18— Borgholm si.c.l.	
Calcareous Well-drained			GROUP 22— Rockwood l. Nebis loam & l.f.s. Beltrami silt l. Taylor cl.l. & v.f.s.l. Kingsley f.s.l. Keewaunee l.			
Poorly drained		GROUP 2— Ontonagon c.	GROUP 6— McDougald f.s.l.	GROUP 7— Spooner v.f.s.l.	GROUP 19— Bergland c.l. Chilgren c.l. Wildwood si.c.l.	

[1] In this table: c. = clay; f. = fine; l. = loam or loamy; s. = sand or sandy; si. = silt or silty; st. = stony; v. = very

here based on soil profile features; whether it also corresponds to differences in aspen growth and plant indicators will appear later.

In the arrangement of the cross-classification in table 11, the attempt is made to follow a systematic progression of certain important factors of the habitat. Thus, in progressing from left to right, whether in the main headings or in their subdivisions, there is always an increase in soil moisture in one form or another, and under each main heading the heavier-textured types are to the right of the less moisture-retentive. The glei soil types with high water table are placed to the right of those without glei horizons and with deep ground water. The peat with excessive moisture appears at the extreme right, preceded to the left by those soil types which also have excessive moisture but not in sufficient amount for the formation of thick peat.

Similarly, in passing from higher to lower categories, in column 1 (character of C horizon) there is a progressive decrease in permeability associated

chiefly with texture and to a less degree with lime content. The relative position of rock and clay groups may be questioned, and in this case there is more variation within the groups than between them. On the whole, however, it seems that the rock areas are somewhat better drained than most of the types with clayey substrata.

The blanks in this classification are partly and perhaps wholly due to the limited variety of habitats sampled. Certainly a slight extension of the region sampled would have disclosed soils of the Miami series in eastern Wisconsin which would fall in the space for xeric, weak A_2 with clayey, calcareous C horizon; and of the Longrie series, in the space for xeric with weak A_2 and calcareous rock C horizon.

The significance of these groups in relation to habitat and growth factors has already been discussed in part in the preceding paragraph and in earlier pages in connection with the influence of texture and geological formation on habitat factors. Soil moisture in this grouping is still one of the most important factors, being controlled to a large degree by the texture of the different layers of the profile, including the C horizon.

The distinction between calcareous and noncalcareous subsoils is somewhat complex in relation to the growth factors. For one thing, a higher content of lime in any part of the profile improves the physical condition of soil, contributing to favorable granular structure in fine-textured soils and increasing the retentive capacity of sandy soils. It tends to render certain mineral nutrients more available. It reduces the hydrogen ion concentration. It stimulates the oxidation processes, and thereby the decomposition of organic matter, both carbohydrate and nitrogenous materials. Nitrogen fixation by the nodule bacteria of the Leguminosae increases with increase in lime content of the soil, and active basic material is essential for the biological transformation of ammonia to nitrate nitrogen. In a region of humid climate such as the one under consideration, the influence of lime in the soil is the resultant of several or all of these effects in combination. Ample evidence is available of the beneficial effects of lime on plant growth in acid soils. The work of Valmari (1921) in Finland, mentioned in an earlier section, demonstrated it for the yield of forests of pine and birch. The higher site indices in the same texture class on the high-lime gray drift as compared with the low-lime red drift are probably the result of greater lime content in the soil. The lime content of the C horizon is used and is believed to be the most useful criterion of the influence of lime because in almost all of the soils sampled the weathering process has removed most of the lime from the A and upper part of the B horizon to a depth varying from 2 to 5 feet. In the soils with calcareous C horizon, a relatively ample supply of lime is within reach of the deeper roots. Indirectly, this supply tends to counterbalance a possible deficiency in the upper horizons because the lime is taken up by the deeper roots, transported to the leaves, returned to the surface layers of the soil when the leaves fall and decompose, and again carried downward in the leaching process.

The glei horizon, when present, is evidence of intermittent and prolonged saturation of the soil from that depth downward by ground water. Ordinarily this horizon is found at depths of 1 to 3 feet. In the heavier-textured, moisture-retentive soils it tends to be an unfavorable factor of the habitat, doubtless because it contributes to deficient aeration. In sandy soils, on the contrary, an ample moisture supply within reach of the roots is almost always beneficial in obviating damage or mortality in critical periods of drought and in stimulating growth at other times.

Finally, the degree of development or podsolization of the A_2 horizon requires some discussion in its relation to habitat and growth factors. In the Russian work on the degradation of tchernozem, reviewed by Glinka (1927), the development of the podsolic profile under the influence of forest cover in place of the black soils of the steppes has been considered unfavorable to the growth factors. In Scandinavia and western European countries, the podsol profile under a layer of raw-humus has been associated with poorer growing conditions and lower forest yields than has the brown-earth profile with a mull layer and higher nutrient contents in the upper horizons. These conditions, however, do not correspond to those in the region under consideration. For one thing there is no raw-humus on the soils of the aspen community and, in its absence, it is by no means certain that the podsolization process is now going on in these soils. On the contrary, it seems likely that the reverse process may be in progress by which the podsolic profiles formed under an earlier and different climate and vegetation are now being transformed into mull, brown-earth profiles under the influence of a relatively mild, dry climate and of deciduous forest vegetation. If this is the case and the podsolic profiles are only relics, little importance can be ascribed to them as indicating growing conditions of the habitats.

Actually it appears that the well-developed podsolic profiles of the areas sampled include the more rather than the less favorable habitats in comparison with the profiles having weakly developed A_2 horizon. The result of this comparison, however, seems to be caused not so much by the intensity of the podsolization and degradation process in the podsolic soils as by the past and present conditions in the weakly podsolized profiles which have been unfavorable to the podsolization process. In this latter group on the xeric side are the excessively drained sands where the percolation of water is so free and rapid that podsolization is slow and ineffective. On the hydric side are the soils with high water table in which excessive moisture has prevented podsolization. In both cases the same factors which have affected the soil development have acted directly rather than indirectly through the soil-forming processes to render the habitats unfavorable for plant growth. Thus the soils with podsolized profiles remain as a group of less unfavorable rather than of more favorable soils, and there is no conflict with the well-supported and generally accepted theory that podsolization is a process of degradation.

The 22 soil-profile groups thus formed, although they are not edaphic units of the same degree as the soil types, still have homogeneity in respect to the several important soil characteristics upon which the classification is based. Moreover, the number of groups is reduced to such a point that sufficient plots are available in most of them to permit biometric analysis.

CORRELATION WITH SITE INDEX AND DIFFERENTIATION OF SOIL-PROFILE GROUPS

The distribution of the site-index values for each of the soil-profile groups, with indices of little significance omitted, is shown in figure 13. In table 12

TABLE 12. CORRELATION RATIO BETWEEN 22 SOIL-PROFILE GROUPS AND SITE INDEX

Soil-profile group	Plots (n)	Mean site index (m_I)	m_I-M_I	$(m_I$-$M_I)^2$	$(m_I$-$M_I)^2 n$
	Number				
1. A$_2$ weak, C sandy, acid, sands and fine sands, xeric	8	47.6	—14.9	222.0	1,776.0
4. A$_2$ weak, C rock, acid, loams, xeric	18	54.7	— 7.8	60.8	1,094.4
3. A$_2$ weak, C sandy, acid, loamy fine sands or sandy loams, xeric	11	54.9	— 7.6	57.8	635.8
5. A$_2$ strong, C rock, acid, no glei, mesic	7	55.0	— 7.5	56.3	394.1
2. A$_2$ weak, C clayey, calcareous, clays	9	55.3	— 7.2	51.8	466.2
6. A$_2$ strong, C clayey, calcareous, no glei, drainage poor	2	55.5	— 7.0	49.0	98.0
7. A$_2$ strong, C clayey, calcareous, glei	3	56.7	— 5.8	33.6	100.8
8. A$_2$ weak, xeric, C sandy, calcareous, sands	10	56.8	— 5.7	32.5	325.0
9. A$_2$ weak, hydric, C clayey, calcareous	9	59.2	— 3.3	10.9	98.1
10. A$_2$ weak, xeric, C clayey, acid, sandy loam	4	61.0	— 1.5	2.3	9.2
11. A$_2$ strong, C. clayey, acid, glei	1	61.0	— 1.5	2.3	2.3
15. A$_2$ strong, C sandy, acid, no glei	19	61.8	— .7	.5	9.3
13. A$_2$ strong, C sandy, acid, glei	5	62.0	— .5	.3	1.3
12. A$_2$ strong, C sandy, calcareous, no glei	14	62.1	— .4	.2	2.2
14. A$_2$ weak, xeric, C rock, acid, sands	5	62.8	.3	.1	.5
17. A$_2$ weak, xeric, C sandy, calcareous, sandy and fine sandy loams	3	63.3	.8	.6	1.9
16. A$_2$ weak, hydric, A$_0$ thick	1	64.0	1.5	2.3	2.3
18. A$_2$ weak, hydric, A$_0$ thin, C clayey, acid	1	66.0	3.5	12.3	12.3
21. A$_2$ strong, C clayey, acid, no glei, sandy loams and heavier	24	66.7	4.2	17.6	422.4
20. A$_2$ weak, hydric, A$_0$ thin, C sandy, calcareous	5	68.4	5.9	34.8	174.0
22. A$_2$ strong, C clayey, calcareous, sandy loams, and heavier, no glei	66	68.9	6.4	41.0	2,706.0
19. A$_2$ strong, C sandy, calcareous, glei	5	71.0	8.5	72.3	361.5
$\Sigma n(=N)$	230	....	......	....	......
$\Sigma[(m_I$-$M_I)^2 n]$	..	....	......	....	8,693.6

$$\sigma M_I = \sqrt{\frac{\Sigma[(m_I - M_I)^2 n]}{N}} = 6.15 \qquad\qquad \eta = \frac{\sigma M_I}{\sigma_I} = 0.795$$

$$\sigma_I = \sqrt{\frac{\Sigma_I{}^2 - M^2{}_I}{N}} = 7.74$$

$$M_I = 62.5$$
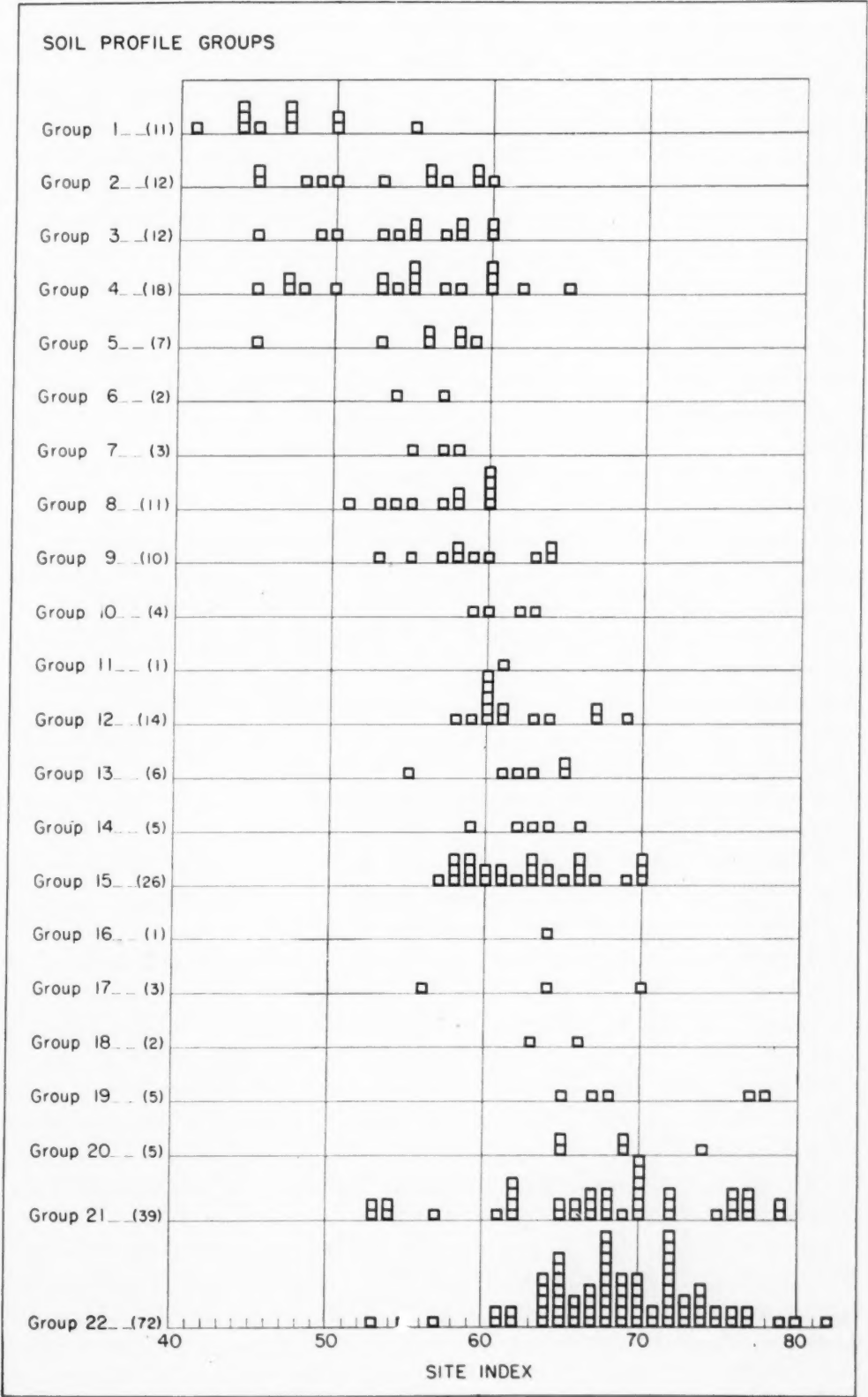
FIG. 13. Distribution of site indices by soil-profile groups.

these are arranged in ascending order of mean site index. The three site-index groups having the lowest mean site indices in the series are all xeric, with weak development of the A_2 horizon, and acid (used in the sense of non-calcareous for the sake of brevity). The fourth soil-profile group is also acid and the rock substratum at shallow depths seems to offset the less unfavorable characteristics indicated by moderate moisture conditions and strong development of the A_2 horizon. The fifth has a weak A_2 and, although calcareous, is rendered unfavorable by the impervious and poorly aerated clay texture on a clayey parent material. Starting at the upper end of the series, the two highest groups are both calcareous with strong A_2 horizons, one with a sandy substratum and high water table, the other with clayey substratum and favorable texture (sandy loam or heavier) in the upper layers. The third is also calcareous but is a hydric group with weak A_2 on a sandy parent material. The fourth is acid with strong A_2 and good texture conditions on a clayey substratum. Various combinations of characteristics typify the intermediate groups.

It is evident from what has been said and from an examination of table 12 that no one profile feature by itself has sufficient weight to enable a prediction of habitat productivity. Furthermore, different combinations of features, more or less favorable in their significance ad acting with different intensities, give rise to a series of groups whose relative position in the scale of productivity could not easily be forecast. Certain indications as to the significance of the different profile features in relation to the growth factors of the habitat may, however, be derived from the mean site-index scale. Xeric conditions tend to be unfavorable for the growth of aspen, especially if they are intensified by sandy surface and subsoil and associated with a poor development of the A_2 horizon. Mesic conditions tend to be favorable. Hydric conditions tend to be favorable except where they are accompanied by deficient drainage. A strong development of the A_2 horizon is more likely to be associated with good growth, and a weak A_2 with poor growth. A calcareous subsoil tends to be more favorable than a noncalcareous. A sandy C horizon is unfavorable in association with sandy surface layers in xeric habitats but generally favorable in hydric habitats. A clayey subsoil tends to be favorable for the growth of aspen except when associated with deficient drainage. A rock substratum at shallow depths is generally unfavorable. Surface texture classes of sands, clays, and peat tend to be less favorable than the intermediate classes with certain exceptions caused by counteracting conditions of subsoil texture or moisture.

The correlation ratio between the 22 profile groups and mean site index and the essential figures for its computation are shown in table 12. The number of plots used for the calculation was limited to the same 230 which were used in the combined texture-surface formation groups so that the correlation ratios might be comparable.

This correlation ratio of 0.795 indicates a high degree of relationship between site-index and soil-profile groups. It is decidedly higher than the best correlation previously established—that of 0.699 with the combined texture and geological formation groups. In other words, profile groups in terms of the features which have been used in the classification afford a better basis for the prediction of site index or productivity of habitat than any of the other groups which have been tried.

The next step is to see how many and which of these groups are distinct from one another, as judged by the significance of the differences between their means. The process and method are the same that were used for the texture-surface formation groups. The numbers from figure 13 and table 12 are used to designate the profile groups. The essential figures are tabulated in table 13. The differences that are discussed in the following paragraph may be visualized by referring to figure 13.

TABLE 13. SIGNIFICANCES OF DIFFERENCES BETWEEN MEAN SITE INDEX VALUES OF SOIL-PROFILE GROUPS

Profile groups	$M_{I_2} - M_{I_1}$	n_2	n_1	n	t	P	Significance of difference
2 - 1	7.7	8	7	15	3.5	0.01	+
4 - 1	7.1	17	7	24	3.3	.01	+
8 - 4	2.1	9	17	26	1.12	.28	—
9 - 4	4.5	8	17	25	2.20	.04	+
9 - 8	2.4	8	9	17	1.37	.2	—
10 - 9	1.8	3	8	11	.80	.4	—
10 - 8	4.2	3	9	12	2.31	.04	+
14 - 10	1.8	4	3	7	1.18	.3	—
17 - 10	2.3	2	3	5	.61	.6	—
21 - 17	3.4	23	2	25	.79	.4	—
21 - 14	3.9	23	4	27	1.22	.2	—
21 - 10	5.7	23	3	26	1.60	.1	—
21 - 19	4.3	23	4	27	1.28	.2	—
20 - 17	5.1	4	2	6	1.34	.2	—
20 - 14	5.6	4	4	8	2.82	.02	+
22 - 14	6.1	65	4	69	2.36	.02	+
22 - 17	5.6	65	2	67	1.64	.1	—

Group 1 is found to be significantly different from group 2 or 4, the next lowest in mean site index. This group of xeric acid sands with weak A_2 horizon therefore may stand by itself, distinct from any of the other groups. The next significant difference is found between groups 9 and 4. At the same time, 8 and 4 and 9 and 8 are not significantly different insofar as the variability of the site indices is concerned. It appears then, on this basis, that groups 2, 3, 4, 5, and 6 could be combined, and that 7 and 8 might be placed either with this combination or with group 9. Group 10 and those above it are significantly different from 8 and those below, but 10 is not significantly different from 9. There is some doubt therefore whether 9 should be included with 7 and 8 or with 10 and 11. Above these, the groups form a rather gradually increasing series without marked differences up to 19, 20, and 22. These

three are significantly different from group 14 and those with site index lower
than 14. Even 21 and 10 are not demonstrably different, and therefore all
the intermediate groups, 11, 12, 13, 14, 15, 16, 17, and 18, may be considered
as parts of a single grouping with respect to mean site index. This leaves a
final grouping of 19, 20, and 22. On the basis of their variability therefore,
the 22 groups could be condensed into 4 or possibly 6 classes which would
have significant differences between but not within the groupings. However,
this is a greater degree of condensation than is needed, and before it is ac-
cepted the groupings will be examined to see if widely and unreasonably
diverse groups are being combined.

Some genetic relationship should exist to justify combining these soil
groups, and such relationships may be seen most readily by referring to
figure 12. In that cross-classification, soil groups along the same horizontal or
along the same vertical element tend to be more closely related than those
in different rows or columns. With this as a guide to logical relationships,
the groupings indicated by lack of significant differences in mean site index
may be reexamined. One of the objects sought is to establish 12 groupings
of soil profiles, so that the correlation ratio for the 12 groups and the 230
samples may be compared with that for the texture-surface formation groups
based on the same numbers, in order to avoid any discrepancy in the com-
parison which might be caused by the use of 12 and 22 groups respectively.

Group 1, the sands with weak A_2 on acid sandy subsoil, may be left as a
single group. Out of the combination of groups 2 through 7, 3 and 4 are
both xeric with poorly developed A_2 horizon and acid subsoils. Groups 4
and 5 are both on a noncalcareous rock substratum. There is therefore some
genetic relationship and justification in a composite of groups 3, 4, and 5.
Groups 2, 6, and 7 are related in that all three are on a clayey, calcareous,
poorly drained parent material and therefore may logically be grouped. At
the same time these three could not reasonably be combined with the preceding
groups, although with respect to mean site index they are not significantly
different. Group 8, xeric sands with weak A_2 horizon and acid sandy C
horizon; group 9, wet, poorly drained soils with weak A_2 and clayey cal-
careous C horizon; and group 10, sandy loams with weak A_2 and clayey, non-
calcareous C horizon, are genetically distinct and may be left as separate
groups. A combination of groups 11 and 13 is based on the characteristics
common to both—a glei horizon, strong A_2, and acid C horizon. Group 12
and 15 both have strong A_2, no glei, and sandy C horizon, so that they may
logically be combined. Groups 14 and 17 form a composite, with poorly
developed A_2 horizon and xeric environment in common.

This leaves only groups 16 and 18 out of the biometrically undifferentiated
series from 11 through 18, and they are combined because both are wet soils
with poorly developed A_2 and noncalcareous C horizon. Groups 19 and 20
are genetically related in having developed upon a more or less hydric sandy

calcareous parent material and are therefore combined. This leaves the final combination of groups 21 and 22, both with strong A_2 and no glei horizon on clayey subsoil.

The foregoing 12 composite groups were used for another calculation of correlation ratio between mean site-index and soil-profile groupings, with the essential figures and results shown in table 14. The figure of 0.788 for the correlation ratio between soil-profile groups and site index based on 12 classes is almost identical with that based on 22 groups (0.795) and is comparable with and superior to the value of 0.699 derived from the combined texture and surface-formation groups when correlated with site index. The significance of the difference between these two correlation ratios is indicated by the ratio of their difference to the standard deviation of that difference. Algebraically this is expressed as

$$\frac{\eta_1 - \eta_2}{\sqrt{\dfrac{\sigma^2 \eta_1}{N_1} + \dfrac{\sigma^2 \eta_2}{N_2}}}$$

The standard errors of the correlation ratios are determined from the relation

$$\sigma_\eta = \frac{1 - \eta^2}{\sqrt{N}}$$

This formula is based on the assumption, which is not strictly true, that the distribution of the correlation ratio is normal. However, when η and N are large, as in the present instance, the inaccuracy in the standard error from

TABLE 14. CORRELATION RATIO BETWEEN 12 SOIL-PROFILE CLASSES AND MEAN SITE INDEX

Soil-profile classes	Plots (n)	Mean site index (m_I)	$m_I - M_I$	$(m_I - M_I)^2$	$(m_I - M_I)^2 n$
	Number				
1	8	47.6	−14.9	222.0	1,776.0
3, 4, 5	36	54.9	− 7.6	57.8	2,080.8
2, 6, 7	14	55.6	− 6.9	47.6	666.4
8	10	56.8	− 5.7	32.5	325.0
9	9	59.2	− 3.3	10.9	98.1
10	4	61.0	− 1.5	2.3	9.2
11, 13	6	61.8	− .7	.5	3.0
12, 15	33	62.0	− .5	.3	9.9
14, 17	8	63.0	.5	.3	2.4
16, 18	2	65.0	2.5	6.3	12.6
21, 22	90	68.3	5.8	33.6	3,024.0
19, 20	10	69.7	7.2	51.8	518.0
$\Sigma n (= N)$	230				
$\Sigma[(m_I - M_I)^2 n]$	...	....	....	....	8,525.4

$$\sigma M_I = \sqrt{\frac{\Sigma[(m_I - M_I)^2 n]}{N}} = 6.09 \qquad \eta = \frac{\sigma M_I}{\sigma_I} = 0.788$$

$$\sigma_I = \sqrt{\frac{\Sigma_I^2 - M^2_I}{N}} = 7.74$$

$$M_I = 62.5$$

this cause is not likely to invalidate the use of the measure. For $\eta_1 = 0.788$ and $N = 230$, $\sigma_{\eta_1} = 0.025$. For $\eta_2 = 0.699$ and $N = 230$, $\sigma_{\eta_2} = 0.034$. Then, $\sigma_{\eta_1 - \eta_2} = 0.003$. The ratio of the difference, 0.089, to 0.003 is 30 so that the difference is unquestionably significant. The soil profiles therefore offer the most reliable basis of any of the soil groupings which have been tried for the classification of the habitats according to their productivity for the growth of aspen.

Before taking up a fifth classification of the habitats of the aspen community, based on the plant indicators, and comparing all five of them, it is necessary to consider in some detail the associated vegetation and the possibilities of its use for purposes of classification.

ANALYSIS OF ASSOCIATED VEGETATION

In several respects the plant indicators, including all the associated species found in the aspen community, are more difficult to treat satisfactorily in relation to habitat than are the soil and growth factors. In the first place there are 236 species which were recorded in the aspen community and from 10 to 50 of them were found on each plot. Each of these species has its own evolutionary adaptation and reaction to the different complexes of growth factors represented in the individual habitats. Unfortunately, some of the factors which influence the plants could not be eliminated or held constant, either as a whole or in the categories of a classification. Differences in light penetrating the aspen canopies of different densities unquestionably influenced the occurrence of certain species. The range of light intensities did not extend to complete sun and sky light, for plots were taken only where the aspen was sufficiently well represented to give character to the community and where it was at least 16 years old. The densities of the aspen canopy did, however, vary considerably, a fact which may underlie some of the variations between plots.

Some of the plant enumerations of individual plots are more or less incomplete owing to seasonal changes in the vegetation. Obviously, an examination in May will not reveal some of the late summer species, and September lists will not include all those of early spring. The frequencies of some of the distinctly seasonal species are doubtless too low for this reason. However, it does not seem likely that any considerable errors in the uses made of the records of associated vegetation will be incurred from this cause.

The vegetation is also influenced by the time which has elapsed since the last fire, which in the aspen community is one year more than the age of the dominant aspens. Areas were avoided where fire scars at the bases of trees indicated that fire had burned since the establishment of the aspen stand. The restriction of the sample areas to stands more than 15 years old allowed ample time for the aspen to have established its dominance, for the disap-

pearance of most of the transitory pioneers which follow fires, and for the attainment of a relatively slow rate of vegetational change.

Notwithstanding these facts there will evidently be differences in the plants between plots less than 30 years old and those over 50 years owing to the greater length of time for vegetational development. As the aspen stands grow older, invading species from the succeeding stages in the succession gradually become established and some of the relic species from the preceding stages disappear. The effect of these floristic changes associated with differences in the age of aspen is somewhat obscured by the presence of species supposedly characteristic of a later stage in the succession in young stands of aspen in company with pioneer species. This frequent occurrence is apparently due to the past fire history of the area. A hot fire which completely covered the area, or repeated fires at short intervals, eliminated relic species from previous forest stages except those which came up from the roots or underground parts which were not killed by the fires. In many places, however, the aspen started after a light fire which did not completely cover the area or kill all the pre-existing vegetation. In such cases, relic species are found in the aspen community from its inception in association with the pioneers which have started from light wind-borne seed, or from the underground parts of the previous generation. Actually a considerable number of the most common species in the community, such as Corylus and *Aralia nudicaulis,* belong to this latter group.

Admitting the varying influences of past fire history and age of the aspen on the composition and abundance of the different species in the associated vegetation, it would still be very difficult 16 to 85 years after the origin of the community to determine in each sample area how the individual species happen to be there. Moreover it is doubtful whether such a determination would do more than support the obvious statement that the older the aspen, the more frequently and commonly are found plants indicating a change in vegetation toward a succeeding stage in the natural succession.

The associated vegetation is analyzed by species according to the frequency of its occurrence in any particular group. The frequency is expressed numerically as the percentage which the number of occurrences in a group bears to the total number of plots in that group or in all groups. This is the "constancy" concept of Braun-Blanquet and Pavillard (1930), although it is hardly distinct in this use from the frequency or frequency percent of Raunkaier (1918), more commonly found in American literature. The indicator value of a species is not, however, always proportional to its frequency. Several of the species which have the highest frequencies are so universally present in all the habitats that they are almost valueless as indicators of habitat differences. At the other extreme a number of species with very low frequencies are found so rarely in the aspen community, that, even if their presence were proved to indicate rather specifically a certain habitat or group

TABLE 15. VEGETATION FREQUENCIES IN COMBINED TEXTURE-SURFACE FORMATION GROUPS

Species	Group Number											
	1	2	3	4	5	6	7	8	9	10	11	12
Abies balsamea	43		85	92	73	31	50	75	23	49	31	41
Acer rubrum	43	80	15	8	27	38	8	25		9	14	21
A. saccharum			10	25	9	19	25			14	14	20
A. spicatum			60	8	55		29		15	26	12	31
Actaea rubra		20	5							3		8
Alnus incana			40	42	36	19	17	50	31	11	19	16
Amelanchier spp.	14		25	50	27	13	21	50	15	26	17	30
Amphicarpa monoica						6	4			6		
Anaphalis margaritacea											2	
Anemone quinquifolia											2	7
Apocynum androsaemifolium						13			15	3		8
Aralia nudicaulis	14	20	85	33	73	19	50		54	43	33	61
Asarum canadense			3	8			4	25	23	6	7	13
Asplenium filix-femina			5				17			26	31	23
Aster macrophyllus	86	100	100	75	100	75	83	50	77	69	86	71
Betula lutea					9		17	25		3	2	
B. papyrifera	86	80	100	92	91	88	75	75	15	80	62	69
Caltha palustris										3		
Carex sp.								50		6		2
Carpinus caroliniana							4			3		
Carya cordiformis							4					
Chamaedaphne calyculata											2	
Chimaphila umbellata							8					
Circaea alpina												2
Clintonia borealis		20	60	33	64	6	50	25	31	46	19	44
Comptonia asplenifolia	57	20				13					5	
Coptis trifolia								25		3	2	2
Cornus canadensis	43	40	80	58	91	44	58	25	23	51	31	33
C. candidissima				8								
C. rugosa		20	15	8	27		21		77	23	38	38
C. stolonifera								75			2	2
Corylus rostrata	71	80	100	50	73	63	67	50	46	63	86	72
Crataegus rotundifolia											10	2
Cypripedium parviflorum											2	2
Diervilla lonicera	71	60	60	33	82	44	48	25	23	34	19	39
Dirca palustris							4					2
Epigaea repens			22	8	27	6	4		8			2
Epilobium angustifolium			25	42		19	4		54	9		5
Epipactis pubescens												2
Equisetum arvense			5	8	18		8	25	8	6	5	7
Fragaria virginiana	43	40	30	58	45	56	58	50	100	49	57	59
Fraxinus nigra							4	50		9	2	7
F. pennsylvanica var. lanceolata				17		6	8		8	9	21	25
Galium triflorum			30		9	19	4	25	85	14	12	43
Gaultheria procumbens	71	20				44	4		8	6	7	2
Geum virginianum												2
Gramineae	29	20		42		38	25	25	23	11	41	21
Hepatica triloba		20	5	17			4			11	2	16
Impatiens pallida			5		9						2	
Iris versicolor								25				
Juglans cinerea							1					
Larix laricina	14		10	8	9		8	50		3	5	3
Lathyrus ochroleucus }		20	30	33	9	6	17		8	9	7	26
L. venosus }												
Ledum groenlandicum					9							
Linnaea borealis			25			6	4	50			5	
Lonicera canadensis			5	8	9				8	3	5	7
Lycopodium complanatum	14		20		13		8				2	
L. obscurum var. dendroideum	29		35	8	27	25	29		8	29	12	5
Maianthemum canadense	29	20	25		9	6	17	50	54	14	21	33
Melampyrum lineare	14					6						
Mitchella repens						6	8			3		
Mitella nuda			5					25	8		1	7
Nemopanthus mucronata	14											
Onoclea sensibilis												2
Osmunda claytoniana												7
Ostrya virginiana				8			8			9	2	3

Species	1	2	3	4	5	6	7	8	9	10	11	12
						GROUP NUMBER						
Parthenocissus vitacea						6					2	
Pedicularis canadensis						6						
Petasites palmatus			10	25		6	13		15	11	2	15
Picea canadensis	43		75	92	55	31	46	25	8	40	17	23
P. mariana	43		35	25	36	13	21	25	8	17	12	8
Pinus banksiana	29		45	17	64	13	13			17	26	2
P. resinosa	71	60	35	42	27	44	25			11	26	5
P. strobus	100	80	60	67	55	87	42	23	8	29	33	25
Polygonatum biflorum			15		36		8			11	5	15
Populus balsamifera						6	4	25		6	2	15
Prunus americana										3	10	5
P. pennsylvanica	43	40	10	17	5	31	13	25	8	11	5	2
P. serotina	14	20				13	8			6	7	5
P. virginiana		40	15		36	6			38	31	19	39
Pteris aquilina	86	60	45	42	45	50	50	25	23	46	48	41
Pyrola elliptica			5	8			8			3	2	11
Quercus alba							8			3		
Q. borealis	29	20		17		38	13			14	10	7
Q. ellipsoidalis		20										
Q. macrocarpa		20				13	4		31	17	45	38
Rhus toxicodendron		20				6	4		23	3	7	7
Ribes cynosbati			5	8	9		8		15	11	5	18
R. triste								25				
Rosa blanda			40	33	36	19	25	25	85	31	17	39
Rubus argutus (?)	29		5	8	18	19	8			3	2	2
R. parviflorus			5	8	9		4		15		5	
R. pubescens			5				4	50	8	11	21	16
R. strigosus							4			3		7
Salix spp	43	20	55	50	27	19	4	25		20	17	10
Sanguinaria canadensis										3		2
Sanicula marylandica												2
Smilacina racemosa							8		8		5	15
Sorbus americana			5		18		4		23	3		2
Sphagnum spp			5				4	50		3	5	3
Streptopus longipes	14		10		9	6			23	14	5	8
Taxus canadensis			5				4		8			
Thalictrum dioicum		20				13	13		23	20	43	51
Thuja occidentalis			33		9	6	13	50		6	7	2
Tilia americana				8			17		8	9	10	26
Trientalis americana			15		9		4	50	15	9	10	15
Trillium grandiflorum						6					2	8
Tsuga canadensis						6					5	
Ulmus americana						6	8		23	6	26	38
Uvularia grandiflora						13	4	25	8	3	5	16
Vaccinium pennsylvanicum	86	20	25	17	36	25	8			9	7	
Viburnum acerifolium												2
V. affine var. hypomalacum												10
V. lentago								25		3		3
V. trilobum												5
Viola spp				8				25	23	3	2	10
Waldsteinia fragarioides	29	60				13	4					
Zanthoxylum americanum												2

of habitats, they would have little value in the characterization of those habitats. Certain species with intermediate frequencies are actually the most useful indicators of growth and habitat differences.

The plants associated with aspen either individually or in groups may be analyzed as dependent, when site index or habitat groups are used as the independent variable; or the plant groups may be used as the independent variable when they are combined in classes based upon the vegetation itself without regard to habitat. Both methods of analysis have been tried and will be discussed, when the plants are considered, first, as the dependent variable

with groupings of site index and soil, and second, as the independent variable.

As a matter of convenience for reference to individual species, and because phylogenetic relationships are of minor importance in relation to habitat and aspen growth, the lists of species are arranged in alphabetical order of the initial letters of the genera and of the species within a genus, except where the order of magnitude of their frequencies is an important consideration.

PLANT INDICATORS AND COMBINED SOIL TEXTURE AND SURFACE FORMATION GROUPS

The habitat groups based on the combination of soil texture and geological formation have been shown to be superior to either soil class or surface formation in relation to height growth of aspen, and the same superiority for the same reasons would undoubtedly appear in the relations to plant indicators. For that reason the two latter groupings have not been analyzed separately in relation to the associated vegetation. Moreover, it will appear from the analysis of the combined groups whether any significant relationships would be likely to be derived from the separate groups.

The frequencies or the percentages which the numbers of occurrences bear to the total number of plots in each soil group are shown in table 15. The most striking thing in this table is the fact that almost all of the common species are represented with high frequencies in almost all soil groups. In other words, the common species are not characteristic of any one soil group exclusively or even of any two or three related groups. In spite of this first and justifiable impression, there are differences in the magnitudes of the frequencies, and it will be worth while to consider each soil group separately to see which species, if any, can be considered at all characteristic. For this purpose, those species will be selected as characteristic which have the highest frequency in that group as compared with any other group, and those as common which have high frequencies in the group although not as high as in some other soil group. This use of the term "characteristic" does not correspond exactly to that of Braun-Blanquet and Pavillard (1930), who restrict it to certain degrees of exclusiveness of the occurrence of a species in different plant associations. Table 16 lists, for each of the 12 groups, the characteristic species arranged in descending order of their frequencies.

In this way it is possible to show an apparent significance of the different species as indicating certain soil groups. A part of the characteristic species do show a tendency on the average for many or very large areas of a given soil group to represent that group of habitats rather than any other. For any single sample area, however, the plants which may be found have very uncertain reliability in indicating the habitat group to which the area belongs. For example, on one plot belonging, according to the character of the soil and

TABLE 16. CHARACTERISTIC SPECIES OF 12 DIFFERENT SOIL GROUPS IN THE ASPEN COMMUNITY

Group 1. Sands and Fine Sands on Red-Drift Outwash (7 Plots)

Characteristic species	Frequency	Common species	Frequency
	Percent		*Percent*
Pinus strobus	100	Betula papyrifera	86
Vaccinium pennsylvanicum	86	Aster macrophyllus	86
Pteris aquilina	86	Corylus rostrata	71
Gaultheria procumbens	71	Diervilla lonicera	71
Pinus resinosa	71	Prunus serotina	14
Comptonia asplenifolia	57		
Picea mariana	43		
Prunus pennsylvanica	43		
Rubus argutus (?)	29		
Waldsteinia fragarioides	29		
Nemopanthus mucronata	14		

Group 2. Sandy Loams and Heavier Soils on Red-Drift Outwash (5 Plots)

Aster macrophyllus	100	Betula papyrifera	80
Acer rubrum	80	Corylus rostrata	80
Prunus virginiana	40	Pinus strobus	80
P. serotina	20	Diervilla lonicera	60
Actaea rubra	20	Pinus resinosa	60
Hepatica triloba	20	Pteris aquilina	60

Group 3. Red-Drift Fine Sands, Sandy Loams, and Loams on Rock (20 Plots)

Aster macrophyllus	100	Abies balsamea	85
Betula papyrifera	100	Cornus canadensis	80
Corylus rostrata	100	Picea canadensis	75
Aralia nudicaulis	85	Clintonia borealis	60
Acer spicatum	60	Diervilla lonicera	60
Salix spp.	55	Pinus strobus	60
Lycopodium obscurum var. dendroideum	35		
L. complanatum	20		
Taxus canadensis	5		
Sphagnum sp.	5		

Group 4. Clay Loams and Clays on Lake-Bed Clay (12 Plots)

Abies balsamea	92	Betula papyrifera	92
Picea canadensis	92	Aster macrophyllus	75
Amelanchier sp.	50	Pinus strobus	67
Gramineae	42	Cornus canadensis	58
Lathyrus ochroleucus }	33	Fragaria virginiana	58
L. venosus }		Alnus incana	42
Acer saccharum	25		
Petasites palmatus	25		

Group 5. Red-Drift Fine Sandy Loams and Silt Loams on Rock (11 Plots)

Aster macrophyllus	100	Betula papyrifera	91
Cornus canadensis	91	Abies balsamea	73
Diervilla lonicera	82	Aralia nudicaulis	73
Clintonia borealis	64	Corylus rostrata	73
Polygonatum biflorum	36	Acer spicatum	55
Epigaea repens	27	Picea canadensis	55
Lonicera canadensis	9	Pinus strobus	55
Ledum groenlandicum	9	Equisetum arvense	18

Group 6. Sands on Sandy Moraine or on Lake-Washed Sandy Till (16 Plots)

Characteristic species	Frequency	Common species	Frequency
	Percent		*Percent*
Quercus borealis	38	Betula papyrifera	88
Populus grandidentata	6	Aster macrophyllus	75
Pedicularis canadensis	6	Pinus strobus	75
		Corylus rostrata	63
		Fragaria virginiana	56
		Pteris aquilina	50
		Cornus canadensis	44
		Caultheria procumbens	44
		Pinus resinosa	44
		Diervilla lonicera	44

Group 7. Fine Sands and Red-Drift Sandy Loams on Sandy Moraine or on Lake-Washed Sandy Till (24 Plots)

Acer saccharum	25	Aster macrophyllus	83
Betula lutea	17	Betula papyrifera	75
Chimaphila umbellata var. cisatlantica	8	Corylus rostrata	67
Mitchella repens	8	Cornus canadensis	58
Carpinus caroliniana	4	Fragaria virginiana	58
Carya cordiformis	4	Abies balsamea	50
Dirca palustris	4	Aralia nudicaulis	50
Juglans cinerea	4	Clintonia borealis	50
Taxus canadensis	4	Pteris aquilina	50

Group 8. Peat (4 Plots)

Cornus stolonifera	75	Abies balsamea	75
Alnus incana	50	Betula papyrifera	75
Carex sp.	50	Aster macrophyllus	50
Fraxinus nigra	50	Corylus rostrata	50
Larix laricina	50	Fragaria virginiana	50
Linnaea borealis	50	Maianthemum canadense	50
Onoclea sensibilis	50		
Rubus pubescens	50		
Sphagnum sp.	50		
Thuja occidentalis	50		
Trientalis americana	50		
Betula lutea	25		
Coptis trifolia	25		
Equisetum arvense	25		
Iris versicolor	25		
Mitella nuda	25		
Populus balsamifera	25		
Ribes triste	25		
Viburnum lentago	25		

Group 9. Clay Loam on Lake-Washed Clayey Till (13 Plots)

Fragaria virginiana	100	Aster macrophyllus	77
Galium triflorum	85	Aralia nudicaulis	54
Rosa blanda	85	Mitella nuda	8
Cornus rugosa	77		
Epilobium angustifolium	54		
Maianthemum canadense	54		
Asarum canadense	23		
Rhus toxicodendron	23		
Sorbus americana	23		
Streptopus longipes	23		
Viola sp.	23		
Apocynum androsaemifolium	15		
Rubus parviflorus	15		
Taxus canadensis	8		

Group 10. Gray-Drift Sands and Red-Drift Sandy Loams and Fine Sandy Loams on Till, Clayey Moraine, or Lake-Washed Clayey Till (35 Plots)

Characteristic species	Frequency	Common species	Frequency
	Percent		*Percent*
Ostrya virginiana	9	Betula papyrifera	80
Amphicarpa monoica	6	Aster macrophyllus	69
Caltha palustris	3	Corylus rostrata	63
Sanguinaria canadensis	3	Cornus canadensis	51
		Lycopodium obscurum var. dendroideum	29

Group 11. Sandy Loams on Gray Drift and Fine Sandy Loams and Heavier Soils on Sandy Moraine or Lake-Washed Sandy Till (42 Plots)

Quercus macrocarpa	45	Aster macrophyllus	86
Asplenium filix-femina	31	Corylus rostrata	86
Prunus americana	10	Betula papyrifera	62
Crataegus rotundifolia	10	Fragaria virginiana	57
Tsuga canadensis	5	Pteris aquilina	48
Anaphalis margaritacea	2		
Cypripedium acaule	2		
Parthenocissus vitacea	2		

Group 12. Gray-Drift Sandy Loams and Fine Sandy Loams and Heavier Red-Drift Soils on Till, Clayey Moraine, or on Lake-Washed Clayey Till (61 Plots)

Thalictrum dioicum	51	Corylus rostrata	72
Ulmus americana	38	Aster macrophyllus	71
Tilia americana	26	Betula papyrifera	69
Fraxinus pennsylvanica var. lanceolata	23	Aralia nudicaulis	61
Ribes cynosbati	18	Fragaria virginiana	59
Uvularia grandiflora	16	Galium triflorum	43
Smilacina racemosa	15	Clintonia borealis	44
Pyrola elliptica	11	Prunus virginiana	39
Viburnum affine var. hypomalacum	10		
Trillium grandiflorum	8		
Anemone quinquefolia	7		
Osmunda claytoniana	7		
Rubus strigosus	7		
Viburnum trilobum	5		
Sanicula marylandica	5		
Lathyrus venosus	3		
Circaea alpina	2		
Epipactis pubescens	2		
Geum virginianum	2		
Viburnum acerifolium	2		
Zanthoxylum americanum	2		

surface formation, to group 7, the following plants were found, each characteristic of the soil group indicated by number after the name:

Acer saccharum, 7	*Polygonatum biflorum,* 5
Aralia nudicaulis, 3	*Populus grandidentata,* 6
Aster macrophyllus, 2	*Pteris aquilina,* 1
Carex (pedunculata ?), 4	*Pyrola secunda,* 7
Betula lutea, 7	*Quercus borealis,* 6
Cornus canadensis, 5	*Rubus (argutus ?),* 1
Diervilla lonicera, 5	*Thuja occidentalis,* 8
Fragaria virginiana, 9	*Tilia americana,* 12
Mitchella repens, 7	*Tsuga canadensis,* 11
Oryzopsis asperifolia, 4	*Ulmus americana,* 12
Pinus strobus, 1	*Viburnum acerifolium,* 12

Summarizing by soil groups, group 7 has four characteristic species, groups 1, 5, and 12, three each, groups 4 and 6, two each, and groups 2, 3,

8, 9, and 11, one each. Group 7 to which the habitat belongs has a larger
representation than any other, but all the rest of the 12 groups except number
10 are also represented. Not all the individual plots were analyzed in this
way, but this example is believed to be quite representative of the loose nature
of the relationship between individual plant indicator species and the texture-
surface formation groups.

Some of the most common species in the aspen community are so nearly
ubiquitous within the community that they are almost valueless as indicators
of habitat differences. This may be noticed in the "common species" column
of the preceding tabulations of several soil groups by the repeated appearance
of certain species with high frequencies, notably, *Aster macrophyllus, Betula
papyrifera, Corylus rostrata, Fragaria virginiana,* and others to a less extent.
At the other extreme are the characteristic species with very low frequencies
in many of the groups, which may be quite distinctive of that group but are
found so rarely that little reliance can be placed upon them in assigning a
given habitat to its proper group. Of course the chance of finding at least one
of them becomes greater where there are several such species, as in group 12.
On the other hand a species with a low frequency may actually be recorded
as representative of a nontypical habitat within a group and thus have a small
or even a deceptive indicator value. An example of this is afforded by the
occurrence of *Nemopanthus mucronata* on one abnormally wet plot in group
1, although it can not be considered typical of the group 1 habitat.

Summarizing the relation between soil-texture and surface-formation
groups and plant indicators, it may be said first that only a few of the low-
frequency species are confined to, and therefore have specific indicator value
for, a single habitat group. Second, the common species are too nearly ubiq-
uitous in the aspen community to be used as indicators of habitat differences.
Third, although there is a loose relationship, it is not sufficiently close to
predict either the habitat group from the plants present or the plants from the
habitat group.

PLANT INDICATORS AND SOIL TYPES AND SOIL-PROFILE GROUPS

The foregoing rather unsatisfactory correlation between plant indicators
and soil-texture and surface-formation groups may be extended by analogy to
the relationships with soil types and profile groups. In that case, however,
instead of 12 groups, there are 54 soil types and 22 profile groups. These
narrower groupings representing more unified and homogeneous habitat con-
ditions might appear, at first thought, to provide just what is needed for a
close correlation with specific plant indicators. But, even with only 12 broad
habitat categories, it was found that almost all of the plants occurred on several
if not all of the soil groups. This is in agreement with the well-known fact
that every plant is able to adapt itself to a considerable range of environmental
variations. If, then, the 12 broad groups are not sufficiently comprehensive

to include the range of variations for most of the species, it is less likely that the narrower groups of 22 and 54 classes would encompass them. The data support this supposition. Almost every species which occurred on more than one or two plots also represented more than one soil type, and most of them more than one profile group. *Abies balsamea* for example was found on 45 of the 54 soil types, *Acer spicatum* on 28, and even a species of rather restricted habitat, *Larix laricina,* on 13. The same conclusion is applicable here that was arrived at above, namely, that the correlation between plant indicators and soil types or soil-profile groups is not sufficiently close to enable prediction of either one from the other.

The proof of the degree of correlation by biometric methods where 230 species and 54 soil types or even 22 profile groups are concerned would require many times the number of plots which were obtained in this study. If the species and groups or types are combined into a 6-by-6-fold classification, as they will be in a later and slightly different connection and as they have to be for the calculation of the contingency coefficient with the limited material available, the groups become so broad that they lose some of their significance as representing the relation of species to soil types.

NATURAL COMMUNITY PLANT-INDICATOR GROUPS

Whereas the vegetation has thus far been grouped according to predetermined habitat classes, the plant indicators will now be made the independent variable, and groups will be established on the basis of the natural community relations of the plants themselves irrespective of habitat or aspen growth. The communities in the region on habitats like those occupied by aspen have usually been characterized by the predominating tree growth. Using this as a starting point, lists of species of the aspen community also found in each of these other forest communities or types were compiled partly from the writer's own field notes, partly from manuscript notes of others, and partly from published references. For this purpose material from eastern Wisconsin and Michigan was used although it was somewhat outside the area from which the aspen material came. This disadvantage is considered to be outweighed by the advantage of having a larger number of sample areas upon which to base frequency percentages.

The compilation gives the following total numbers of lists or sample areas in each of the communities: Jack pine, 57; Norway pine, 9; white pine, 123; oak, 87; white spruce-balsam, 6; sugar maple, 24; ash-elm, 1; white cedar, 4; tamarack, 3; black spruce, 4; hemlock, 8; and alder-sedge, 3. These numbers are used as the denominators of the fractions for the frequency ratios, the actual numbers of occurrences of each species in a given community forming the numerators.

Each species is then considered to be characteristic of the community in which it has the highest frequency. This corresponds to the concept of Braun-

Blanquet and Pavillard (1930) who include as "characteristic" species those with exclusiveness indices of 5, 4, and 3 in a scale of 5. The characteristic species determined similarly by a percentage scale for each of the foregoing communities are listed below. If a species has equal frequencies in two communities it is included in both of them. Because of the small number of sample areas and the consequently inadequate representations of plants in a few of the communities, they were combined. Thus the alder-sedge was combined with the ash-elm, hemlock with sugar maple, and black spruce with tamarack, making nine communities in all.

Sugar maple community

Actaea rubra
Adiantum pedatum
Allium tricoccum
Amphicarpa monoica
Aralia nudicaulis
A. racemosa
Arisaema triphyllum
Asarum canadense
Aspidium noveboracense
A. spinulosum
    var. intermedium
Asplenium filix-femina
Betula lutea
Botrychium virginianum
Brachyelytrum erectum
Carex brunnescens
C. laxiflora
    var. latiflora
Carpinus caroliniana
Carya cordiformis
Caulophyllum thalictroides
Celastrus scandens
Circaea alpina
Clintonia borealis
Cornus alternifolia
C. rugosa
Corylus rostrata

Crataegus rotundifolia
Desmodium grandiflorum
Dioscorea villosa
Dirca palustris
Equisetum arvense
Fagus grandiflora
Galium aparine
G. asprellum
G. triflorum
Geranium bicknellii
Geum virginianum
Hystrix patula
Juglans cinerea
Lonicera canadensis
L. hirsuta
Luzula campestris
    var. multiflora
Lycopodium annotinum
L. lucidulum
Mitchella repens
Mitella diphylla
Osmunda cinnamomea
Osmorhiza claytoni
O. claytoniana
Ostrya virginiana
Parthenocissus vitacea
Phegopteris dryopteris

P. polypodioides
Phryma leptostachya
Polygonatum biflorum
Prunella vulgaris
Prunus americana
Pyrola elliptica
Quercus borealis
Q. macrocarpa
    var. olivaeformis
Ribes cynosbati
Rubus parviflorus
R. pubescens
Sambucus pubens
Sanguinaria canadensis
Smilacina racemosa
Smilax hispida
Streptopus longipes
Thalictrum dioicum
Tiarella cordifolia
Tilia americana
Trillium grandiflorum
Tsuga canadensis
Uvularia grandiflora
Viburnum lentago
Viola pubescens
Vitis vulpina

Ash-elm community

Acer rubrum
Alnus incana
Caltha palustris
Carex spp.
Cicuta maculata
Cornus stolonifera
Cryptotaenia canadensis
Epilobium palustris
Eupatorium purpureum

Fraxinus pennsylvanica
    var. lanceolata
F. nigra
Gramineae spp.
Ilex verticillata
Impatiens pallida
Iris versicolor
Juncus (tenuis?)
Onoclea sensibilis

O. struthiopteris
Smilacina stellata
Smilax herbacea
Populus balsamifera
Rudbeckia laciniata
Scutellaria lateriflora
Ulmus americana
Viburnum trilobum

Tamarack-black spruce community

Aspidium cristatum
Chamaedaphne calyculata
Chiogenes hispidula
Coptis trifolia
Cypripedium parviflorum

Epipactis pubescens
Larix laricina
Ledum groenlandicum
Mitella nuda
Picea mariana

Ribes prostratum
R. triste
Sphagnum spp.
Vaccinium canadense

White spruce-balsam community

Abies balsamea
Acer spicatum
Clintonia borealis
Cornus canadensis
Epipactis pubescens

Linnaea borealis
Lycopodium obscurum
    var. dendroideum
Mertensia paniculata
Mitella nuda

Picea canadensis
Sorbus americana
Taxus canadensis
Trientalis americana
Viola renifolia

Jack pine community

Amelanchier laevis
Anaphalis margaritacea
Antennaria neodioica
Apocynum androsaemifolium
Aster ericoides
A. lindleyanus
Corylus americana
Diervilla lonicera
Lathyrus ochroleucus

L. venosus
Melampyrum lineare
Nemopanthus mucronata
Oryzopsis pungens
O. asperifolia
Pedicularis canadensis
Physalis lanceolata
Pinus banksiana
Polygala pauciflora

Rosa blanda
Rubus argutus
Salix humilis
Spiranthes gracilis
Steironema ciliata
Veronica virginiana
Viola conspersa
Waldsteinia fragarioides

Norway pine community

Anemone virginiana
Aster cordifolius
A. laevis
Chimaphila umbellata
    var. cisatlantica
Cladonia spp.
Epigaea repens
Epilobium angustifolium
Fragaria virginiana

Galium boreale
Gaultheria procumbens
Habenaria orbiculata
Lycopodium complanatum
Oakesia sessiliflora
Pinus resinosa
Populus grandidentata
Prenanthes alba
Prunus pennsylvanica

Pyrola secunda
P. americana
Quercus alba
Sanicula marilandica
Symphoricarpos albus
Viburnum acerifolium
Vicia americana

White pine community

Anemone quinquefolia
Aquilegia canadensis
Aster macrophyllus
Geranium maculatum
Hepatica triloba
Lonicera dioica
    var. glaucescens
Maianthemum canadense

Mitella diphylla
Monarda mollis
Pinus strobus
Potentilla sp.
Prunus serotina
P. virginiana
Pyrola americana
Ranunculus sp.

Rhus toxicodendron
Rubus strigosus
Trillium cernuum
Viburnum affine
    var. hypomalacum
Zanthoxylum americanum

Oak community

Aronia melanocarpa
Carex (umbellata?)
Comptonia asplenifolia
Convolvulus spithamaeus
Corallorhiza striata

Cornus candidissima
Hammamelis virginiana
Helianthus divaricatus
Lysimachia quadrifolia

Pteris aquilina
Quercus ellipsoidalis
Solidago spp.
Vaccinium pennsylvanicum

White cedar community

Betula papyrifera	Petasites palmatus	Thuja occidentalis
Lycopodium clavatum		

The foregoing lists do not pretend to be complete for the communities represented and they do not necessarily include the most common species in those communities, but they are believed to show the communities other than aspen with which the species of the aspen community are most frequently associated. With these lists as a guide, the species recorded on each aspen plot were allocated to one of these groups and the plot assigned to that group which had the largest representation of species. This process resulted in a division of the aspen plots into 9 groups, which are called natural community groups. Three of these, sugar maple, white spruce-balsam, and white pine, had large representations of plots in comparison with the other six groups. These three groups were then subdivided according to the community represented by the second largest number of species. Thus, within the white spruce-balsam group, those plots which by the plant indicators showed relationship to jack pine or to Norway pine communities were separated from those which had plants chiefly representative of the sugar maple community. In the same way the white pine group was divided into four parts, white pine with jack pine indicators, white pine with white spruce-balsam indicators, white pine with sugar maple indicators, and white pine with tamarack-black spruce-cedar-ash indicators. Similarly the sugar maple group was subdivided into four, one with Norway pine indicators, one with white pine, one with white spruce-balsam, and the fourth with swamp species indicators.

In all this process of grouping and subdivision, it was evident that hardly one of the plant indicators was exclusively confined to any one group. Only the different frequencies of species in different groups served to differentiate between them by means of the associated vegetation. Often the small differences in frequency seem to offer only slight support for distinctions between plots and their allocation to groups; but in the aggregate they seem to have considerable significance, as will appear in the subsequent analysis of the relations of these groups to growth and soils.

The groups also have rather definite successional relations among themselves if it is assumed that the indicator plants have the same successional significance in the aspen community that they would have in the forest communities by the names of which they have been designated. The subdivision of the groups is somewhat finer than that ordinarily used in describing the stages in the succession in the region, and thus a part of them may be thought of as transitions between the usual stages. Furthermore the region happens to be partly in the zone of overlap between the sugar maple-basswood and the spruce-balsam-birch climaxes so that transitions between the two successions as well as between the stages in each one of them are represented.
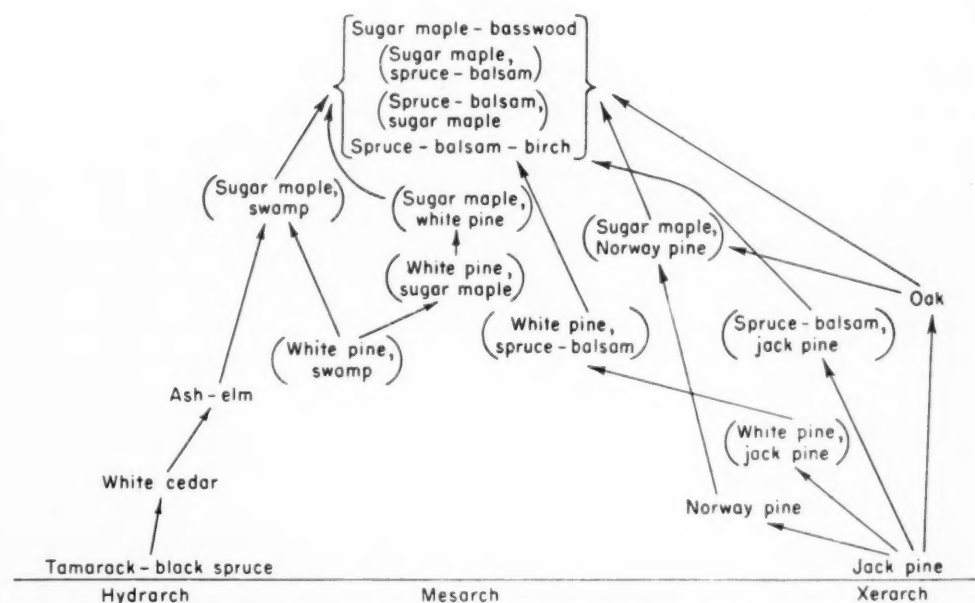
Fig. 14. Successional tendencies in natural community groups of aspen plant indicators. Parentheses indicate transitional stages.

The relation of each of the 16 groups to the successional diagram for the region is shown in figure 14. Evidence in the form of invading and relic species of the trees themselves is available in these plots in support of the relations shown, but it is not sufficiently relevant to the present subject to justify the lengthy presentation that would be required. The pioneer stages preceding the tree stages in the successions and those not represented in the data from the aspen community are omitted from the diagram.

If these groups are arranged as nearly as possible in ascending order of the successional stages toward the climaxes, combining the xerach and hydrarch stages in the same ascending scale, their sequence would be that of the first column in the following tabulation:

Successional sequence	*Site-index sequence*
1. Tamarack-black spruce	1. Norway pine
2. Jack pine	2. Tamarack-black spruce
3. Norway pine	3. White cedar
4. White cedar	4. Jack pine
5. White pine, jack pine	5. Spruce-balsam, jack pine
6. Oak	6. White pine, jack pine
7. Ash-elm	7. White pine, spruce-balsam
8. White pine, swamp	8. Oak
9. Spruce-balsam, jack pine	9. Spruce-balsam, maple
10. White pine, spruce-balsam	10. White pine, swamp
11. White pine, maple	11. Maple, Norway pine
12. Maple, Norway pine	12. Maple, white pine
13. Maple, white pine	13. White pine, maple
14. Maple, swamp	14. Maple, spruce-balsam
15. Spruce-balsam, maple	15. Maple, swamp
16. Maple, spruce-balsam	16. Ash-elm

Obviously the relative positions of any two adjacent groups cannot be determined exactly and might be reversed, but roughly this order represents that of the natural succession. As a corollary, then, it should also represent a series of habitats in which each successive one has been built up by the addition of humus toward a more mesic and favorable environment until a later stage of more exacting species can invade and gain possession. If this be true, then it should follow that the foregoing order of groups should be that of increasing favorableness with respect to site index and growth of aspen. It will be interesting shortly to make the comparison, although it may be noted at this point that the ascending order of favorableness for the stages of natural succession would not necessarily for that reason be identical for the growth of aspen, a single community which normally takes its place as a pioneer tree stage of the mesarch succession.

The mean site indices for each of these 16 natural community plant-indicator groups were computed in the usual way. The values in ascending order determine the arrangement of groups in the site-index sequence, so that comparisons of the two sequences may be made. The larger discrepancies in the two sequences are represented by the noticeable differences in position of the spruce-balsam, jack pine; white pine, spruce-balsam; spruce-balsam, maple; and ash-elm. Apparently the wet conditions of habitat of the last community, or rather of the plants associated with the community, are favorable for the growth of aspen, notwithstanding the fact that they are more hydric than mesic and some distance removed from the climax habitat.

The other three groups are all characterized by the presence of large proportions of the species associated with the white spruce-balsam group. Furthermore, they are all three decidedly lower in the site-index sequence than in the successional sequence. This suggests that the white spruce-balsam, although it is a climax community, represents relatively unfavorable conditions for the growth of aspen in comparison with those of the maple climax. This might have been predicted from a consideration of the comparative distribution and environmental conditions of the two climaxes. The spruce-balsam is the northern conifer-forest climax associated with the cold climate, short growing season, and less favorable edaphic conditions of latitudes chiefly north of the United States. Within this region, the habitats which it occupies would naturally be less favorable than those with locally warmer climate, longer growing season, and more favorable soil-forming processes of the deciduous forest climax, here near its northern limit. If then the groups with spruce-balsam indicator plants were placed lower in the successional order than those with maple indicators, the series arranged according to the natural succession would correspond more closely with that determined by the mean site index of the aspen. On the whole there is a decided indication that, as the stages of natural succession, distinguished by the plant indicators, ap-

proach the climax, the habitats as measured by the growth of aspen are progressively more productive.

CORRELATION WITH SITE INDEX AND DIFFERENTIATION OF NATURAL COMMUNITY GROUPS

With these plant-indicator groups, it is now possible to calculate the correlation ratio with site index as the dependent variable, in the same way that similar measures were obtained with the groups based on soil or geological features. The present groups, however, have been established independently of soil characteristics except as the soils may have indirectly influenced the frequencies of the plants. The groups, arranged in ascending order of mean site index, are shown in table 17, with the essential figures for the computation of the correlation ratio.

TABLE 17. CORRELATION RATIO BETWEEN NATURAL COMMUNITY PLANT-INDICATOR GROUPS AND SITE INDEX

Plant-indicator group	Plots (n)	Mean site index (m_I)	$m_I - M_I$	$(m_I - M_I)^2$	$(m_I - M_I)^2 n$
	Number				
1. Norway pine	23	52.1	−10.8	116.6	2,681.8
2. Tamarack-black spruce	10	53.0	− 9.9	98.0	980.0
3. White cedar	7	55.1	− 7.8	60.8	425.6
4. Jack pine	9	55.4	− 7.5	56.3	506.7
5. Spruce-balsam, jack pine	27	58.0	− 4.9	24.0	648.0
6. White pine, jack pine	12	58.5	− 4.4	19.4	232.8
7. White pine, spruce-balsam	5	59.2	− 3.7	13.7	68.5
8. Oak	4	62.8	− .1	.01	.0
9. Spruce-balsam, maple	39	63.4	.5	.25	9.9
10. White pine, swamp	8	63.9	1.0	1.0	8.0
11. Maple, Norway pine	7	65.4	2.5	6.3	44.1
12. Maple, white pine	26	67.5	4.6	21.2	551.2
13. White pine, maple	16	67.8	4.9	24.0	384.0
14. Maple, spruce-balsam	6	68.8	5.9	34.8	208.8
15. Maple, swamp	35	69.0	6.1	37.2	1,302.0
16. Ash-elm	25	69.6	6.7	44.9	1,122.5
$\Sigma n (= N)$	259				
$\Sigma[(m_I - M_I)^2 n]$	...	....	......	....	9,173.9

$$\sigma M_I = \sqrt{\frac{\Sigma[(m_I - M_I)^2 n]}{N}} = 5.95 \qquad \eta = \frac{\sigma M_I}{\sigma_I} = 0.761$$

$$\sigma_I = \sqrt{\frac{\Sigma I^2}{N} - M_I^2} = 7.82$$

$$M_I = 62.9$$

The correlation ratio of 0.761 shows a considerable degree of relationship between site index and the plant-indicator groups. In other words, the natural community groups have a real value in the prediction within limits of the average site index or growth of the aspen. In comparison with the correlation ratios between site index and the soil groups, this one is distinctly higher than the 0.699 for combined texture and surface-formation groups but not very different from the 0.788 of the soil-profile groups. The difference

between 0.788 and 0.761 may be tested for significance in the same way that 0.788 has been shown to be significantly different from 0.699. The standard error of 0.788 is 0.025 as before. For 0.761 and N of 259, σ_η is 0.026. Then, the standard deviation of the difference is 0.0023 and the actual difference, 0.027, is twelve times this figure, making the correlation ratio with soil-profile groups significantly higher than that with plant-indicator groups. Thus the plant-indicator groups are only slightly inferior to the soil-profile groups as a basis for the differentiation of habitats with respect to their productivity for the growth of aspen.

Having determined the correlation, it will now be interesting to see whether the individual plant-indicator groups are significantly different one from another as judged by the variability of the site-index values within the single groups and, if not, which ones may be combined. Figure 15 shows the distributions of site-index values for each group and table 18 contains the figures for the calculation of the significance of differences.

Groups 1, 2, 3, and 4 may be combined insofar as their variability is concerned because 1 and 4, the extremes, are not significantly different. Group 5 is significantly different in mean site index from group 1 and is therefore considered to belong to a second combined grouping. Group 9 is the first one above 5 which is significantly different from it; wherefore groups 5, 6, 7, 8, and 9 may be combined. However, since 9 is significantly different from 6 and there is a noticeable gap between 7 and 8, two combined groupings were adopted, one including numbers 8, 9, and 10, and the other, 5, 6, and 7. Group 12 is significantly different from 9, although not from 10, and 16 is significantly different from 10, although not from 12. Evidently then, groups 12, 13, 14, 15, and 16 may be combined, leaving only the question of whether 11 should be placed with this group or with 8, 9, and 10. To sum up, the biometrically significant differences between these plant-indicator groups would not distinguish more than four groupings.

Is there any biological basis for these groupings? In the first 4 groups,

TABLE 18. SIGNIFICANCE OF DIFFERENCES BETWEEN MEAN SITE-INDEX VALUES OF NATURAL COMMUNITY PLANT-INDICATOR GROUPS

Group	$M_{I_2} - M_{I_1}$	n_2	n_1	n	t	P	Significance of difference
4 – 1	3.3	8	22	30	0.96	0.3	—
5 – 1	5.9	26	22	48	3.55	.01	+
7 – 4	3.8	4	8	12	.61	.5	—
7 – 3	4.2	4	6	10	1.39	.2	—
8 – 7	3.6	3	4	7	1.55	.2	—
8 – 5	4.8	3	26	29	1.59	.1	—
9 – 5	5.4	38	26	64	3.75	.01	+
9 – 7	4.2	38	4	42	1.59	.1	—
9 – 6	4.9	38	11	49	2.73	.01	+
12 – 9	4.1	25	38	63	2.99	.01	+
12 – 10	3.6	25	7	32	1.59	.1	—
16 – 12	2.1	24	25	49	1.35	.2	—
16 – 10	5.7	24	7	31	2.20	.03	+
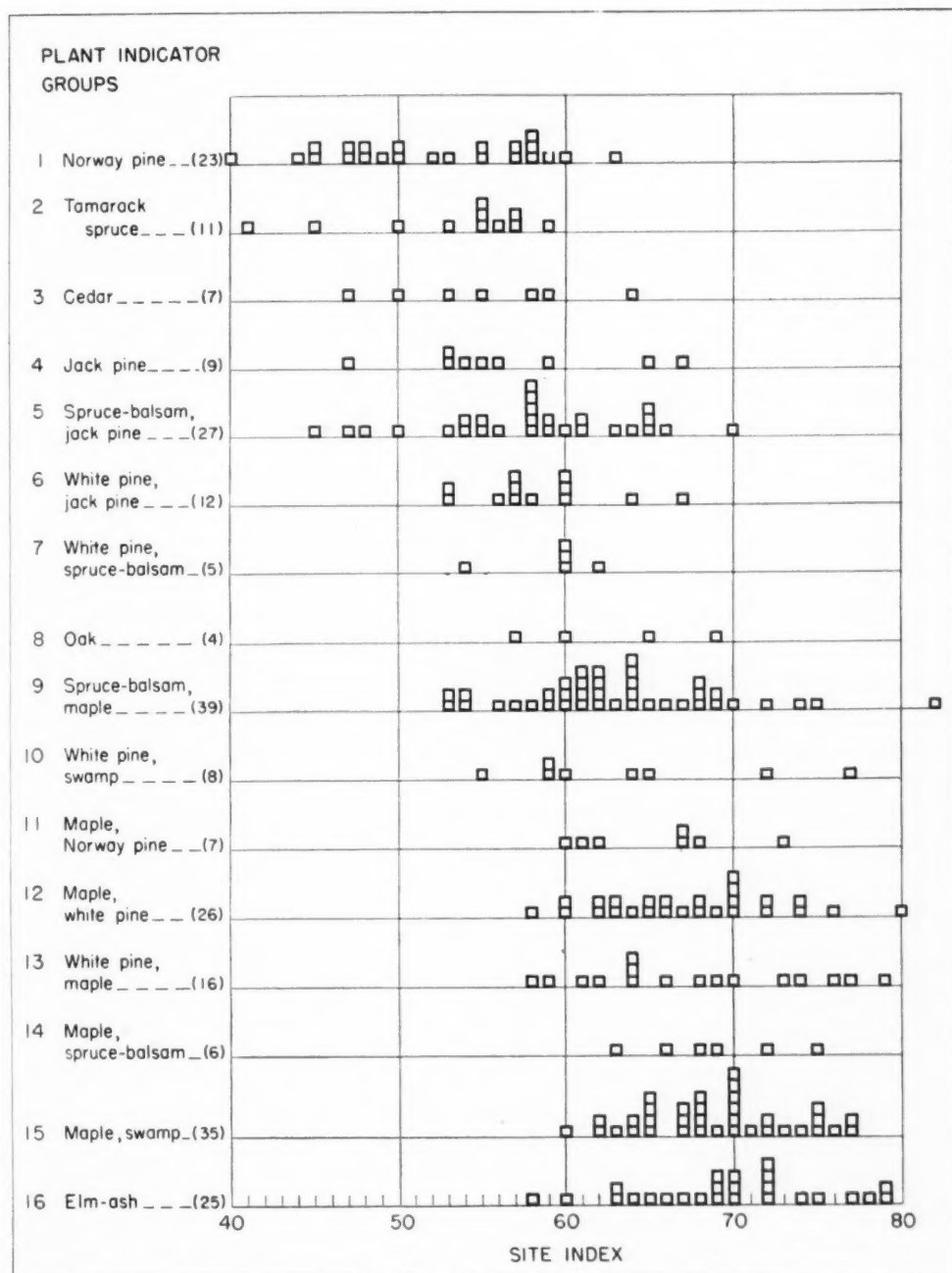
FIG. 15. Distribution of site indices by plant-indicator groups.

that of Norway pine may logically be combined with jack pine and tamarack-black spruce with white cedar, but there is no reason for combining the first two with the last two except that they happen to have closely corresponding values of the mean site index for aspen. Groups 5, 6, and 7 have sufficient similarities in their composition so that their combination does not violate the

usual ideas of relationship. Groups 8, 9, and 10 contain rather diverse elements and little biological justification can be adduced for their combination. Groups 11 through 16, with the exception of 16, have the sugar maple associates strongly represented in their composition, which gives them a degree of biological unity. Group 15, sugar maple, swamp is also related to the ash-elm group so that all six groups have some biological homogeneity. On the whole, the plant indicator-site index analysis, in respect to the number of significantly different groupings which it distinguishes, is not noticeably different from the soil groupings, about four being differentiated in each case; and, in this as in the previous analyses, these do not have complete physical or biological homogeneity.

RELATIONS OF PLANT-INDICATOR GROUPS AND SOIL-PROFILE GROUPS

There are 16 plant-indicator groups and 22 soil-profile groups in the classifications which seem to have the greatest biological unity. There would thus be 352 cells or categories in a cross-classification with these two series as variables. With only 265 plots, the use of such a degree of refinement disperses the data too thinly for an adequate measure of the relationship to be obtained. If the number of soil-profile groups is reduced to 11, however, the same that were used in the second determination of the correlation with site index, except that the two small groups 16 and 18 and 19 and 20 have been combined into one, some indication of the relation between the two groupings may be obtained. The numbers of plots in each of the cells of such a cross-classification are shown in figure 16. Evidently the distribution is not uniform. There is a noticeable concentration in the upper left-hand and a more significant one in the lower right-hand cells. This tendency may be interpreted roughly by the statement that, as the habitats classified by the soil profiles become more favorable, the frequency of occurrence of aspen plots increases from those characterized by the xeric and hydric to those with mesic or hydro-mesic plant indicators, chiefly sugar maple associates.

For the calculation of a biometric measure of the degree of association between these two nonquantitative series, a further concentration of the groups becomes necessary. For the determination of the coefficient of contingency, the material does not justify more than a 6-by-6-fold classification. Accordingly the plant-indicator groups and the soil-profile groups of figure 16 were further combined into six categories each, on the basis of the biological and genetic relationships, respectively. For the plant groups, numbers 1, 4, and 8, Norway pine, jack pine, and oak were combined as representing the three most xeric communities. Groups 2 and 3, tamarack-black spruce and white cedar, together form the most hydric group. Groups 5, 6, and 7 may be considered a white pine-white spruce-balsam-jack pine grouping with a certain degree of homogeneity. Groups 9 and 10, white spruce-balsam-maple and white pine-swamp, occupy somewhat similar hydro-mesic habitats and have a

PLANT INDICATOR
GROUPS

1 Norway pine _ _(23)

2. Tamarack_ _ _(10)

3. Cedar_ _ _ _ _(7)

4. Jack pine _ _ _(9)

5 Spruce-balsam,
   jack pine_ _ _(28)

6. White pine,
   jack pine_ _ _(13)

7. White pine,
   spruce-balsam_(6)

8. Oak_ _ _ _ _ _(4)

9. Spruce-balsam,
   maple_ _ _ _(39)

10. White pine,
    swamp_ _ _ _(8)

11. Maple,
    Norway pine_ _(7)

12. Maple,
    white pine_ _(27)

13. White pine,
    maple_ _ _ _ _(16)

14. Maple,
    spruce-balsam(7)

15. Maple, swamp_(35)

16. Elm-ash_ _ _(26)

| 1 | 3,4,5 | 2,6,7 | 8 | 9 | 10 | 11,13 | 12,15 | 14,17 | 16,18 19,20 | 21,22 |

PLOTS IN SOIL PROFILE GROUPS

FIG. 16. Distribution of plots by plant-indicator and soil-profile groups.

number of species in common, associated particularly with *Abies balsamea*. Groups 11, 12, and 13 are the sugar maple-white pine-Norway pine transitions preceding the climax. The sixth grouping is composed of numbers 14, 15, and 16, the sugar maple-spruce-balsam, sugar maple-swamp, and ash-elm, the deciduous climax and the two groups most closely related to it in the hydric succession.

Similarly, for the soil-profile groups numbers 1, 3, 4, 5, and 8 form a combination of xeric soils on sandy or rock parent material, generally non-

calcareous with weak A_2 horizon. Groups 2, 6, 7, and 9 are poorly drained soils on clayey calcareous subsoil. Groups 10, 14, and 17 include the remaining groups with weak A_2 horizon not included in the first combination. Numbers 12 and 15 are characterized in common by a strongly developed A_2 horizon without a glei horizon on sandy parent material. The combination of groups 11, 13, 16, 18, 19, and 20 includes all the glei and hydric soils on sandy or noncalcareous clayey subsoils. The sixth and last grouping of numbers 21 and 22 includes the largest number of soil types, but all of them are characterized by strong A_2 horizons, without glei, on clayey parent material.

In combining the soil-profile and plant-indicator groups into these less numerous categories, something of homogeneity in the resulting groupings has evidently been sacrificed. From this point of view the process is undesirable and tends to obscure biological and physical differences. At the same time, however, in connection with the analyses of site-index relations with these two classifications, it has been shown that the differences between the individual groups are in many instances not significant biometrically. The differences between the nonquantitative groups cannot be determined in the same way. If they could be, it seems likely that the same paucity of significant differences in the 16 and 22 or 12 group classifications would be found. It has been pointed out that the 16 plant-indicator groups include transitional stages between those usually recognized in successional studies. On the whole, therefore, it is not improbable that the 6-by-6 classification may approximate the number of groupings which are really distinguishable and useful. Even if this is not wholly true and the broader groupings partially fail to differentiate between distinct categories, it does not necessarily follow that the 6-by-6 classification will not give a reliable indication of the degree of relationship between soil-profile and plant-indicator groups. As direct evidence, it may be recalled that the change from 22 to 12 soil-profile groups in the correlation ratio with site index changed the value only from 0.795 to 0.788. In any case it will be interesting to see what degree of association between the two series of six categories each is indicated by the coefficient of contingency. The essential figures and the method of calculation, adapted in part from Yule (1924), are given in table 19.

The probability of less than 0.01 may be interpreted to mean that the difference between the actual and the computed distributions is significant. The contingency coefficient of 0.62 indicates a significant degree of association. The maximum possible value of the coefficient for a 6-by-6-fold table is 0.913, which would be obtained if all the plots were concentrated in the diagonal row of cells from upper left-hand to lower right-hand corner of the table. The conclusion previously suggested is, therefore, confirmed that the soil-profile and plant-indicator categories are distinctly associated.

In the upper section of table 19, there is a simultaneous progression from

Table 19. Coefficient of Contingency as Developed From Soil-Profile Groupings and Plant-Indicator Classes

DISTRIBUTION OF PLOTS BY NUMBER

Plant-indicator classes	Soil-Profile Groupings						
	1,3,4, 5,8	2,6,7,9	10,14,17	12,15	11,13,16, 18,19,20	21,22	n_p
1,4,8........	20	7	1	7	0	1	36
2,3..........	6	7	C	1	3	0	17
5,6,7........	23	4	3	7	3	7	47
9,10.........	7	5	6	6	3	20	47
11,12,13.....	1	2	2	9	0	36	50
14,15,16.....	1	2	0	9	11	45	68
n_t........	58	27	12	39	20	109	....
N........	..	..	..	..	..	..	265

DISTRIBUTION COMPUTED ACCORDING TO TOTALS $= \dfrac{n_t \cdot n_p}{N}$

1,4,8........	7.9	3.7	1.6	5.3	2.7	14.8	36.0
2,3..........	3.7	1.7	.8	2.5	1.3	7.0	17.0
5,6,7........	10.3	4.8	2.1	6.9	3.5	19.3	46.9
9,10.........	10.3	4.8	2.1	6.9	3.5	19.3	46.9
11,12,13.....	10.9	5.1	2.3	7.3	3.8	20.6	50.0
14,15,16.....	14.9	6.9	3.1	10.0	5.1	28.0	68.0

$$S = \Sigma \left[\frac{n^2pt}{n_t \cdot n_p} \right] = 427.7 \qquad\qquad \chi^2 = S - N = 162.7$$

Number of degrees of freedom, 5 x 5 = 25. $P = 0.01 -$

$$C = \sqrt{\frac{S-N}{S}} = 0.62$$

left to right and from top to bottom in the soil groups, from the immature, less well-developed and less favorable soils to the mature, well-developed and more favorable soils; and in the vegetation groups, from the early successional stages, both xeric and hydric, to the hydro-mesic subclimax and mesic climax species. The parallelism in the genetic development of the soils and the successional development of the vegetation is marked and is the more noteworthy because the concepts of the dynamic processes of soil formation, of immaturity and maturity, have been evolved independently of the similar concepts in vegetational succession. Inasmuch as the sample plots come from different habitats and do not actually represent the changes in soil and vegetation with time on identical areas, it would be unjustifiable to conclude that the two processes go on step by step and at the same rate. Nevertheless the suggestion is interesting that, given a certain stage in soil formation as indicated by the profile, the species of a corresponding stage in vegetational succession tend to be associated with it. Furthermore, it seems likely that each one of the two processes is influenced in its rate of development by the other.

One further consideration tends to confirm this suggestion. Both plant-indicator and soil-profile groups have been shown to have moderately high correlations with site index. The ascending order of the groups in each of these correlations is indicated approximately by their numerical designations. In table 19, it may be noticed that the numbers of the soil-profile groups increase from left to right and of the plant-indicator groups from top to bottom, the same directions which result in the contingency trend. This affords additional evidence of the association between soil-profile and plant-indicator groups.

RELATIONS OF INDIVIDUAL PLANT INDICATORS AND SITE INDEX

The simplest and most obvious way in which to use plant indicators is as individual species whose presence, absence, or frequency may be found to represent some condition of habitat or growth. The value of individual species as indicators of site index will therefore be examined in some detail. In table 20 the percentage frequency is shown for each species (or genus) in each of the four classes into which the site-index distribution is divided. The frequencies are based on the total number of occurrences of the species in all site-index classes. They are grouped according to the species which had the highest frequencies in each of the four site-index classes so that the species most characteristic of each class are grouped together and arranged within the groups in alphabetical order.

Evidently individual species tend to be associated with certain ranges of site index more often than with others. There are a considerable number which are most frequently associated with the 51-60 and 61-70 site-index classes and relatively few in the two extreme classes. Those species which have the highest frequencies in a certain class usually have frequencies not much lower in one or both of the adjacent classes. The species which have 100 percent frequency in one class are almost all those of which there was only a single record. If additional occurrences had been noted they would doubtless have added representations in other classes. Even species which would be expected to be limited to an extreme and narrow range of habitat and therefore of site index, show considerable variation. For example, *Comptonia asplenifolia,* although it has a high frequency in the 30-50 class, occurs also in the two higher classes. On the contrary, *Acer saccharum,* a climax dominant which would be expected to indicate habitats of high productivity, is represented in all four of the classes, and has a low indicator value. On the whole, the conclusion seems justified that individual species do not characterize the site index of aspen specifically enough to be used for prediction with any degree of confidence, even within a range of as much as 10 site-index units.

The plant-indicator value of individual species is distinctly less than that of groups of species, on the same basis of classification. Furthermore, group-

TABLE 20. FREQUENCY PERCENTAGES FOR INDIVIDUAL SPECIES IN SITE-INDEX CLASSES

Species	Class 30-50	Class 51-60	Class 61-70	Class 71-90
Poor site indicators:				
Chamaedaphne calyculata	100	..	..	..
Chimaphila umbellata	50	..	50	..
Comptonia asplenifolia	72	14	14	..
Lycopodium complanatum	38	38	16	8
Populus grandidentata	50	25	13	12
Quercus ellipsoidalis	50	50	..	..
Rubus parviflorus	50	..	50	..
Fair site indicators:				
Abies balsamea	13	39	38	10
Acer rubrum	11	50	31	8
Amelanchier laevis	5	47	43	5
Aster macrophyllus	9	40	37	13
Betula papyrifera	11	41	36	12
Corylus rostrata	9	42	36	12
Cypripedium acaule	..	100	..	..
Epigaea repens	..	67	22	11
Epilobium angustifolium	..	100	..	..
Equisetum arvense	..	64	36	..
Gaultheria procumbens	40	47	13	..
Hepatica triloba	..	56	33	11
Impatiens pallida	..	100	..	..
Larix laricina	25	33	33	9
Lathyrus ochroleucus and L. venosus	3	52	37	6
Ledum groenlandicum	..	100	..	..
Linnaea borealis	11	56	..	33
Maianthemum canadense	6	37	33	24
Mitella nuda	..	54	23	23
Nemopanthus mucronata	..	100	..	..
Osmunda claytoniana	..	100	..	..
Picea canadensis	14	40	37	9
P. mariana	18	45	32	5
Pinus banksiana	16	54	30	..
P. resinosa	21	53	26	..
P. strobus	21	42	28	9
Polygonatum biflorum	..	52	48	..
Prunus pennsylvanica	31	35	34	..
P. serotina	25	25	25	25
Pteris aquilina	10	41	38	11
Quercus borealis	19	50	19	12
Ribes cynosbati	4	41	33	22
Rubus (argutus?)	17	68	17	..
R. strigosus	..	50	40	10
Salix sp.	20	41	36	3
Solidago sp.	..	80	20	..
Sphagnum sp.	..	44	33	22
Streptopus longipes	..	50	42	8
Taxus canadensis	..	100	..	..
Vaccinium canadense	18	68	14	..
Good site indicators:				
Acer saccharum	8	36	43	13
A. spicatum	2	33	40	24
Actaea	..	40	40	20
Alnus incana	2	33	52	13
Amphicarpa monoica	..	..	100	..
Apocynum androsoemifolium	..	14	43	43
Aralia nudicaulis	5	38	44	13
Asarum canadense	..	37	37	26
Asplenium filix-femina	3	23	49	26
Betula lutea	..	..	84	16
Clintonia borealis	..	39	45	16
Coptis trifolia	21	29	50	..
Cornus canadensis	11	39	44	6
C. (not canadensis)	..	39	43	18
Cypripedium parviflorum	..	..	100	..
Diervilla lonicera	11	33	45	10
Fragaria virginiana	7	37	42	13
Fraxinus nigra	..	44	56	..
F. pennsylvanica var. lanceolata	..	19	55	26

TABLE 20. *(Continued)*

Species	Class 30-50	Class 51-60	Class 61-70	Class 71-90
Galium triflorum	..	36	45	19
Geum virginianum			50	50
Gramineae	10	33	51	6
Iris versicolor			100	
Lonicera canadensis	5	33	52	10
Lycopodium obscurum var. dendroideum	3	41	47	9
Mitchella repens	..		100	
Ostrya virginiana	..	12	75	13
Petasites palmatus	..	38	46	15
Populus balsamifera	..	42	50	8
Prunus americana	..		86	14
P. virginiana		37	47	16
Pyrola spp.	8	25	58	9
Quercus macrocarpa	..	22	52	26
Rhus toxicodendron	..	38	54	8
Rosa sp.	3	15	61	21
Rubus pubescens	..	24	52	24
Smilacina racemosa	..	26	63	11
Sorbus americana	..	38	62	..
Thalictrum dioicum	3	23	52	22
Thuja occidentalis	13	33	47	7
Tilia americana	..	17	57	26
Trientalis americana	..	35	48	17
Tsuga canadensis	..	25	50	25
Ulmus americana	..	7	61	32
Uvularia grandiflora	..	29	47	24
Viburnum spp.	..	37	37	25
Viola spp.	..	11	78	11
Excellent site indicators:				
Carex spp.	..	20	..	80
Carpinus caroliniana	..	..		100
Dirca palustris	..	..	50	50
Onoclea sensibilis	..	..		100
Trillium grandiflorum	..	20	40	40

ings of species according to site-index or soil classifications are less satisfactory than one in which species are grouped according to their associations in natural communities. This is particularly true if the groups are used to establish the relations with both habitat and growth or with more than the one set of factors on which the plant-indicator classification is based.

SUMMARY AND CONCLUSIONS

The records from 277 sample areas of the aspen community in northern Minnesota and northwestern Wisconsin, a region of relatively uniform climate, have afforded the opportunity to evaluate quantitatively the interrelations between habitats, plant indicators, and the growth rate of aspen.

The habitat classifications, according to soil texture, surface geological formation, a combination of texture and surface formation, and soil type and profile groups, represent a series which comprise successively larger proportions of the total number of edaphic factors which influence the floristic composition and growth of plant communities. Texture classes reflect chiefly the aeration and moisture relations in the surface 8 inches. Surface formations express also the aeration and moisture relations, less definitely for the surface but more adequately for the subsoil, and, in addition, the ground water and drainage factors. The combination of texture class and surface formation integrates the factors of the two separate bases for classification.

Soil types and profile groups synthesize all of the factors, physical, chemical, and biological, which influence plants as they do the processes of soil formation.

As a measure of the degree to which each of these classifications corresponds to the growth of the aspen community, the correlation ratios between soil groups and mean site index of the aspen plots of each group, gave the following results:

Basis of classification	Correlation ratio
Soil-texture class	0.573
Surface formations	.640
Soil-texture classes and surface formations	.699
Soil-profile groups (12)	.788

The correlations become successively closer as the soil classifications represent larger proportions of the growth factors of the habitats. The soil profiles offer the best foundation for the differentiation and prediction of the productivity of the different habitats for the growth of aspen.

Site index, a measure of the height growth of dominant aspen, is a better criterion of habitat productivity than is volume growth. This is indicated by the correlation ratio of 0.699 between site index and of 0.461 between volume index and the soil texture-surface formation groups. This superiority obtains notwithstanding the fact that the correlations were based on all the plots for site index and on only the well-stocked plots for volume index, thus in the latter case minimizing the influence of density, one of the important sources of variation in growth rate.

The associations of plants of the aspen community with other natural communities, as determined by the maximum frequency for each plant in the different communities, affords another and independent basis for the classification of the habitats. Classified in this way, the natural community groups have a correlation ratio with the mean site index of aspen of 0.761, superior to any of the soil groupings except the 0.788 with the soil-profile groups. Thus natural community plant-indicator groups rank very close to the soil-profile groups for the prediction of the productivity of the habitats for the growth of aspen.

Tests of the significance of the differences in mean site index of aspen between the categories of the texture-surface formation, soil-profile, and natural community classifications indicate that in each case only about four combinations of groups are distinguishable, as judged by the variability of the site-index values. The fact that this same limitation is derived from three independent sources suggests that, as the number of subdivisions of any habitat classification is increased, a point is reached at which the local and individual variations of soil and vegetation within the categories become as great as the differences between categories. As measured by the growth of

aspen, this point is reached when the combined groupings are so few and broad that they have little physical and biological homogeneity. In several intances they comprise groups of very diverse characteristics except with respect to the growth of aspen. The conclusions may be drawn, first, that the habitats of the aspen community in the region represent about four distinguishable site qualities for the growth of aspen; and, second, that physical or biological classifications of the aspen habitats do not always differentiate productivity classes or site qualities, all of which are distinct in respect to the growth of aspen.

The 54 soil types represent more nearly homogeneous unit habitats than any of the broader categories of classification. At the same time, many of them are not distinguishable as measured by the growth of aspen or by the plant indicators. Their homogeneity is obscured when they are combined into larger groups which have biometrically significant differences. Because this process is necessary in order to use the soil types in relation to the growth of aspen, their value for the purpose is relatively small.

Habitat groups based on edaphic characteristics are not specifically differentiated by individual plant indicators. Only a few of the low frequency species have specific indicator value for individual habitat groups and their infrequent occurrence seriously detracts from their usefulness. The abundant and high frequency species are nearly ubiquitous in the aspen community and therefore have little or no indicator value. The relation between soil groups and individual plant indicators is not sufficiently close to enable the satisfactory prediction of one by means of the other.

If the plant indicators are combined in 16 natural community groups and thereby are related to the 22 soil-profile groups, a certain degree of correlation is obtained, although it cannot be satisfactorily expressed biometrically with the relatively few data available. If these groups are condensed to six in each category, forming as nearly as possible homogeneous classes, a coefficient of contingency of 0.62 is obtained, indicating a significant and, considering the negative findings for the individual plant indicators, a surprisingly close association between the two series.

This association between plant indicator and soil-profile groups may be interpreted by the statement that, as the soils may be considered to form a progressive series from the immature, less well-developed, and less favorable groups to the mature, well-developed, and more favorable groups, so also the vegetation groups, by analogous steps, progress from the early successional stages, both xeric and hydric, to the hydro-mesic subclimax and mesic climax groups. In other words, the stages of the vegetational succession tend to be associated with a corresponding series as represented by the genetic development of the soil profiles.

The site index or growth rate of aspen is not characterized within a sufficiently narrow range for useful predictions by the individual species of the

associated vegetation of the community. Certain infrequent species seem to be relatively specific but have little value because of their uncommon occurrence. Almost all of the high-frequency species are associated with more than half of the total range of site index and therefore have little indicator value. Groups of species which are more representative of certain site-index classes than of others are readily segregated by their frequencies, and in the aggregate these groups have some value as indicators of aspen growth, just as the natural community groups were shown to have a relatively close correlation ($\eta = 0.761$) with site index.

The more important of the foregoing conclusions may be epitomized and brought into relief in a final paragraph. Site index of aspen is a more reliable measure than volume growth, and may be used satisfactorily for the evaluation of the differences and relative productivity of the aspen habitats. Conversely, the habitat groups, which may be established most effectively on the basis of soil profiles, may be used within limits for the prediction of the average growth of aspen. Individual plants of the aspen community do not indicate with sufficient reliability differences either in the habitats or growth rates of aspen. Groups of plant indicators, of which the most satisfactory are those based on maximum frequencies in natural communities other than aspen, together with the soil-profile groups, are the two most useful classifications for the differentiation and for the prediction of the productivity of the different aspen habitats.

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TERMITE NESTS—A STUDY OF THE PHYLOGENY OF BEHAVIOR

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CONTENTS

TERMITE NESTS—A STUDY OF THE PHYLOGENY OF BEHAVIOR

INTRODUCTION

Almost every naturalist who travels in tropical countries observes the striking nests of termites and many figures of these nests have been published (Hegh 1922). The significance of termite nests to biological theory, however, has been only partially stressed, although Darwin (1859) places considerable emphasis upon the evolution of "instinct" as illustrated by "neuter and sterile insects." He states:

But I must confess, that, with all my faith in natural selection, I should never have anticipated that this principle could have been efficient in so high a degree, had not the case of these neuter insects led me to this conclusion. I have, therefore, discussed this case, at some little but wholly insufficient length, in order to show the power of natural selection, and like-wise because this is by far the most serious special difficulty which my theory has encountered. The case, also, is very interesting, as it proves that with animals, as with plants, any amount of modification may be effected by the accumulation of numerous, slight, spontaneous variations, which are in any way profitable, without exercise or habit having been brought into play. For peculiar habits confined to the workers or sterile females, however long they might be followed, could not possibly affect the males and fertile females, which alone leave descendants. I am surprised that no one has hitherto advanced this demonstrative case of neuter insects, against the well-known doctrine of inherited habit, as advanced by Lamarck.

Subsequent writers have referred to Darwin's statement and have used the sterile castes as an argument against the Lamarckian concept (Ball, 1890, 1894; Weismann 1893; Holmes 1911), but the rich recent information made available through greater exploration and systematic study of tropical faunas has not yet been adequately interpreted. I propose, in the following pages, to present the best cases known to me illustrating the principles of evolution as applied to termite nesting behavior.

I am indebted to Mr. G. F. Hill, Senior Entomologist in the Division of Economic Entomology in Australia, an eminent contributor to our knowledge of termites, for the photographs of Australian termite nests. The African nests were photographed by Mr. Herbert Lang while on the Lang-Chapin expedition of the American Museum of Natural History during which he made a splendid collection of termites and took many valuable field notes. The other photographs were taken by the author or under the author's direction.

Studies of north African and European termites were made by the author during the tenure of a John Simon Guggenheim fellowship, during which time Dr. F. Santschi and Dr. F. Silvestri were particularly helpful. Studies

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TERMITE NESTS AS ILLUSTRATIONS OF
BEHAVIOR EVOLUTION

The nests of termites have certain attributes which make them objects of
great biological interest. These may be listed as follows:

(1) The nest structures are morphological expressions of behavior pat-
terns. This quality makes aspects of behavior evolution as visible as mor-
phological evolution and similar principles and terms may be directly applied.
(2) The nest results from the activity of a large number of individuals co-
operating in building, organizing and enlarging the structure. Individual
variation is thus practically cancelled and the nest stands as an expression of
the behavior of a population.

(3) The nest-forming behavior is predominantly an inherited species-pat-
tern. The nests of a given species show striking similarity in material, gen-
eral shape, internal organization and ecological position. In most instances,
the workers which construct the nest have had no contact with workers of
other colonies. The reproductive castes, which do not exhibit complicated
nest-building behavior, fly from the parental nest, pair, and lay eggs which
develop into workers which again establish a nest with the specific char-
acteristics of the parental nest.

(4) The caste which builds the nest in all the higher termites is the sterile
worker helped, in some cases at least, by the larger soldier nymphs. Thus we
have a complete control over any possibility of the inheritance of an acquired
character. No nest-building habit or structural modification of a sterile caste
acquired during ontogeny could be transmitted to the succeeding generation.
This control over any Lamarckian influence is even better than that found in
other social insects. Workers of wasps, bees and ants, although without

socially functional young in most cases, not infrequently lay eggs which, being unfertilized and haploid, develop into fertile males. This is not known among termites. Workers of termites may, therefore, be considered as somatic individuals, physiologically separated from the germ plasm of the reproductive individuals, making a directive influence upon the genetic determiners a practical impossibility.

(5) The nests are definitive enough and at the same time specific enough to give us excellent evolutionary sequences. These may be correlated with the known morphological evolutionary relationships of the species. We have nest sequences of species in the same genus available, information that should give us a clue to the influence of species divergence upon these behavior patterns. In numerous instances we also find nest characteristics common to many species within a single genus or a group of related genera, thus indicating a long stability of the inherited patterns.

(6) Astonishing examples of adaptive modification of the nests together with convergent evolution of nest structure in certain environments present evidence of the force of selection acting upon the inherited patterns.

(7) The evolution of the nesting behavior is one aspect of the evolution of polymorphism. The colony of polymorphic insects has many attributes of the individual multicellular organism and exhibits many interesting parallels to organismal coordination mechanisms and interrelations of parts. Natural selection probably acts upon the colony as a whole more than upon the individual termite.

PRE-ISOPTERAN NESTING BEHAVIOR

The available indications point toward excavation of wood as the primitive nesting behavior. Certain wood-eating roaches, such as *Cryptocercus punctulatus* Scudder, probably represent the closest approach to the activities of the blattoid ancestors of the termites. Cleveland (1934, p. 190) describes the excavations of this roach as follows:

The wood is honeycombed with galleries which, for the most part, run parallel with the grain. In some of the sounder logs, particularly chestnut, which is often very hard, the roaches are seldom found near the outside. * * There is little evidence that they ever leave the log and enter the ground. * * They pass well-formed pellets of dry, woody material which is not utilized in any way for building purposes or for the construction of passage ways, differing in this respect from many species of more highly specialized termites.

With reference to excavations for the ootheca, Cleveland (p. 207) states:

a groove had been made in the wood where none existed before and the ootheca had been carried approximately six inches, placed in the groove, and sealed off so completely that only a portion of one end was visible.

These observations and others indicate the probability that habitations in excavated wood and the care of the eggs, as well as wood-feeding, symbiotic relationship with gut-inhabiting protozoans, and development of a family organization, antedated the origin of the Isoptera.

NESTING BEHAVIOR OF THE KALOTERMITIDAE

Among the living termites, *Mastotermes darwiniensis* Froggatt (Mastotermitidae) is universally admitted to be the most primitive morphologically. However, the descriptions of its nesting activities (Hill 1921, 1925) would seem to indicate an advance over the behavior of kalotermitids usually considered more advanced from a morphological standpoint. As Imms (1919) and Emerson (1926, p. 92) have remarked, in certain morphological details *Archotermopsis* (Kalotermitidae) is more primitive than *Mastotermes*. One may either conclude that *Mastotermes* has undergone evolution toward more intricate behavior after its divergence from the ancestral isopteran stock, or else that degenerative evolution of the behavior patterns has occurred in the Termopsinae and other kalotermitids. With only meager evidence, I am inclined toward the former hypothesis.

From morphological considerations, *Archotermopsis wroughtoni* (Desneux) is the most primitive living member of the Kalotermitidae. The following description of the nest is taken from Imms (1919, p. 126), who also figures the galleries:

Any structure which might be designated a termitarium or nest is absent, and the bulk of the members of a colony are to be found in irregular chambers situated in the decayed portions of a tree trunk. The wood is perforated in various directions by large galleries or tunnels. Certain of these passages pass outwards in a radial direction terminating just beneath the bark, if the latter be present. The majority, however, run in a longitudinal direction following the grain of the wood. The insect does not construct tunnels of cemented material on the surface of the tree trunk or the ground, as is the custom among a very large number of Termites. There is usually, therefore, no outward manifestation of its presence, which probably accounts for the insect having so long remained a rarity. When necessary, however, it closes up crevices by means of a cement of masticated ligneous material, or of excrementous matter held together by salivary secretion. The centre of a colony is occupied by the ova and very young larvae, and in their immediate vicinity the queens and kings are to be found.

The above description also applies to the nests of species in the related genus, *Zootermopsis*, found in the western United States. These species have been classed by Light (1934, v. 136) as "damp-wood termites" because they seem to be more dependent upon moisture than the majority of the Kalotermitidae which are often classed as "dry-wood termites." Both the damp-wood and dry-wood termites may live wholly within excavated wood and usually do not invade the soil, although in certain instances, notably *Kalotermes (Paraneotermes) simplicicornis* Banks, soil excavations may be found (Light 1934, p. 140; 1937).

EXCAVATING BEHAVIOR OF THE KALOTERMITIDAE

Although the excavation of wood is probably the most primitive behavior for the construction of a protected nesting site, the responses to environmental factors are quite intricate. A cork in a test-tube containing a captive colony of *Kalotermes flavicollis* (Fabricius) was invaded by the termites through small openings about the diameter of the larger nymphs. The end of the cork was cut off with a knife and revealed the excavations of the termites (Fig. 1). Through examination of the figure, it will be noted, in the first place, that the galleries are elongated and are strikingly correlated with the spring growth rings, only occasional passageways being found in the summer growth rings. This is probably a reaction to mechanical stimuli, although these rings doubtless differ in chemical composition as well. Secondly, it will be noted that the termites excavate close to the surface, but do not penetrate the surface. The layer between the excavation and the outside is so thin that light shines through when the cork is held up to the light.

FIG. 1. Cork excavated by
Kalotermes flavicollis.

One might classify this phenomenon as a reaction to light, to changes of humidity or to a weakness in the thinner layers of cork. If pieces of wood within a test tube are subject to the attack of termites, no such thin layer is left, thus indicating that the weakened material is not the only factor, although the termites would seem to be sensitive to such differences. Likewise, termites do not avoid light shining through glass test tubes or containers, providing the light is not too hot and the humidity is not lowered materially. Toleration experiments and experiments with a humidity gradient conducted by Williams (1934) indicate sensitivity to humidity in most cases studied, although some of the Kalotermitidae do not seem to be highly sensitive to low humidities. Pending further experimentation, it would seem to me that a change in humidity was the factor dominantly responsible for the separation of the excavations from the exterior. Pillars of corky material are to be seen in the photograph. These have been left around the hollow lenticel pores in the cork running at right angles to the growth rings. Such pillars are probably best interpreted as reactions to changes in humidity.

To what extent the excavating termites respond to stresses and strains in the wood has not yet been satisfactorily determined, although the problem is open to experimental attack. Observations, particularly by those investigating damage to building construction wrought by termites, seem to indicate

that termites will not weaken timbers sustaining weights to the point of
collapse. If such timbers collapse, extra strains have been placed upon them
through storms, earthquakes, or additional weights to which the termites
have had no opportunity to react while making their excavations. Spatial
factors may also play a rôle but have not been much investigated.

There is little to indicate that the presence of the king, queen, young or
eggs influence the excavation activities of the Kalotermitidae. These primi-
tive termites do not have grossly enlarged queens and the reproductive castes
are usually found in galleries approximating the size and general appearance
of the other galleries. Eggs may be found in the cells occupied by or near
the reproductive castes. They may be picked up and gathered into small
groups by the nymphs as has been observed by the author in captive colonies
of *Zootermoposis angusticollis* (Hagen) and *Kalotermes flavicollis*.

CONSTRUCTION BEHAVIOR OF THE KALOTERMITIDAE

Although excavation as the result of feeding activities supplies termites
with a protected nesting site, positive constructions supplement the burrows
in producing habitations even in the most primitive kalotermitids.

After the colonizing flight and subsequent pairing, the reproductive couple
of *Kalotermes minor* Hagen excavates a small hole or cell in available wood
and plugs the entrance. Harvey (1934, p. 225) states: "This plug is a mix-
ture of partially chewed wood and a secretion of the termites which acts as
a cement."

The worker-like nymphs of a mature colony of *Zootermopsis angusticollis*
kept in a quart mason jar built extensive partitions separating cells in the
excavated wood and also connecting the wood with the glass. These parti-
tions were made largely from the pellets of excrement which were cemented
by saliva, and by liquid excrement which was extruded upon the pellets
worked into place by the mouth-parts. Small experimental holes made in
the metal cover of the jar were plugged in a similar manner. The nymphs
would seem to react directly to changes in humidity, although other factors
may also contribute to the cooperative action involved in building a partition.

Such building activities as those described for *Kalotermes* and *Zooter-
mopsis* are probably to be found with little variation throughout the Kalo-
termitidae. In a few instances, permanent runways may be excavated
through soil which enable the termite colony to exploit food resources out-
side the nest. Such runways are not common in the Kalotermitidae, but
have been reported by Light (1934a, p. 311; 1937).

NESTING BEHAVIOR OF THE MASTOTERMITIDAE AND HODOTERMITIDAE

Hill's (1921, 1925) accounts of the nests of *Mastotermes darwiniensis*
leave little doubt that the nesting behavior must be more specialized than

that found in the Kalotermitidae. The nests are subterranean and are not always closely associated with the feeding excavations. Extensive construction and covered galleries are reported; the colonies contain over a million individuals, and foraging termites may destroy wooden materials over a hundred yards from the nest.

Even though this account gives the impression of rather specialized nesting behavior, it would seem to differ quantitatively rather than qualitatively from that of the Kalotermitidae.

The hodotermitids seem to be an offshoot of primitive kalotermitids or possibly pre-kalotermitids. Their social organization indicates considerable specialization beyond that observed in the Kalotermitidae. They have become harvesters and feed largely upon grass; they have an active, pigmented caste with compound eyes which forages on the surface in the day time and is usually considered an adult worker, a caste which seems to be lacking in the Mastotermitidae and Kalotermitidae.

Accompanying the evolution of structure and social integration, we find elaborate nesting behavior transcending anything observed among other primitive termites. Fuller (1915) has given excellent descriptions and figures of the nests of the South African species of this family (also Hegh 1922, pp. 232, 233). The nests of *Hodotermes (H.) mossambicus transvaalensis* Fuller are built in excavated chambers under the surface of the earth. The soil is brought to the surface and dropped in small piles which are distributed by the rain. Fuller (p. 350) states:

The hive-cavities, with one exception, were all sub-spherical, having a horizontal diameter of 24 in. and a perpendicular height of 18 in. The cavities are partitioned by very numerous horizontal and close-set shelves. These are constructed of a thin and very papery substance which does not dissolve in water or in alcohol. The shelves lie one above another with striking regularity, and are attached to a series of clay brackets projecting from the walls. The shelves are not equi-distant apart throughout the cavity, but range from 6 to 15 mm. Innumerable little cylindrical columns of wooden texture, spread over the field of each shelf, hold the whole fabric together. These little columns are not stairways; the insects pass up and down from storey to storey of the hive by short inclines.

Of particular interest is the construction of the supporting columns. It would seem necessary to assume an intricate reaction to strains in the nest material to account for such elaborate architecture.

Nests of *Hodotermes (Anacanthotermes) ochraceus* (Burmeister) which I examined on the outskirts of Kairouan, Tunisia, consisted of soil excavations without surface indications except that the soil particles had been cemented together over the cells near the surface forming a brittle cover which gave off a hollow sound when lightly tapped. Some of these cells were filled with strips of plant epidermis from the stems of surrounding scrub vegetation. A tiny termitid, *Eremotermes indicatus* Silvestri, was

found living in these storage cells feeding upon the food gathered by *H. ochraceus*. Extensive chambers contained all stages of nymphs and all castes of *H. ochraceus*.

A mason jar was filled with soldiers and various sizes of "workers." The smallest was about ½ cm. long and the largest about 1 cm. long. Soil together with strips of plant epidermis collected by the termites was also included. The termites immediately started to construct passageways and galleries and to accumulate the food. The construction was performed by working pieces of dirt moistened by saliva into place with the mouth-parts. No abdominal excretion was observed during the construction activities. All sizes of "workers" including the next to the smallest engaged in the labor.

These data indicate a much more developed nesting behavior in the Hodotermitidae than has been found among the Kalotermitidae. The emancipation from a wood diet, the construction of subterranean galleries, the storage of food, and the subtle manipulation of materials in the construction of complex layers of cells, passageways and supports; all indicate greater elaboration of the inherited behavior patterns than is found elsewhere below the Termitidae.

NESTING BEHAVIOR OF THE RHINOTERMITIDAE

The family Rhinotermitidae was derived, according to the available morphological evidence (Hare, 1937), from a kalotermitid stock fairly closely related to *Stolotermes*. The social development is much more marked than in the Kalotermitidae and a true sterile adult worker caste has become differentiated. Specialization of the worker is accompanied by larger numbers of individuals in the colonies, enlargement in size and reproductive capacity of the queen, incorporation of certain specialized termitophiles into the social community—all indicative of more complex social organization.

Excavations and passageways in the soil enable these insects to reach soil moisture which seems to be necessary for their existence in nature and also enables them to exploit food resources remote from their nests. Because of their adjustment to soil conditions, they are typical "subterranean termites" and have been so classed by Snyder (1920, p. 89).

The development of more elaborate nesting behavior might be expected in this family, but in reality the nests are still largely to be found in excavated galleries in wood with somewhat more complex cells, partitions and covered tunnels than are characteristic of the Kalotermitidae.

The more elaborate nest structures among the Rhinotermitidae are made by certain species of *Coptotermes*. Oshima (1919) has published some excellent figures of the nests of *C. formosanus* Shiraki. He states (p. 333):

The nest consists of a mixture of abdominal excreta and clay or sand, pasted together with a special secretion of the salivary glands. Sometimes

it is rigid and compact and seems like a piece of rock. However, it is inflammable and burns rapidly, leaving a small amount of ash.

Ehrhorn (1934, p. 327, 329) shows photographs of the nests of the same species and Light (1934, p. 142) figures the nests of *C. vastator* Light. Hill (1915, p. 92) gives an excellent description of the nests of *C. acinaciformis* (Froggatt) accompanied by photographs. This species builds conspicuous mounds usually found at the base of a tree or enveloping a stump. The mounds may reach a height of six to eight feet. The walls of these nests are constructed of fine particles of earth and sand firmly cemented together. The walls vary in thickness from two inches near the top to twelve inches near the ground or on the sides. The interior is composed of triturated wood molded into curious forms. Near the ground are found thin-walled horizontal cells serving as the "nursery." Hill also states:

The queen is generally found about three inches from the ground, and about the middle of the nest, in a low domed cell with more or less level floor, from which she cannot excape.

It is apparent that the nests of *Coptotermes* illustrate the use of various materials, the organization around social functions, and reaction to the presence of the queen resulting in the construction of a "royal cell."

During the colonizing period it is necessary that exits from the nest be made in order to allow the imagoes to emerge. Holes are excavated by the workers in all cases observed and the soldiers guard the exits during the emergence of the imagoes. The exits are plugged by the workers at the end of the flight. Two instances of building activity associated with the colonizing flight have been observed. Wood of a beam in a small house three miles from Kartabo, British Guiana, was infested with *Coptotermes testaceus* (L.). On the morning of July 2, 1924, Dr. S. C. Crawford and the writer noticed workers constructing a small shelf about an inch long, a half inch wide and a half inch high, at the mouth of a small excavated hole in the wood on the vertical face of the beam. Soldiers guarded the operations. About two hours later a light rain fell and as it ceased, flying imagoes of the species were noticed. They were soon discovered emerging from the hole in the beam and using the shelf as a platform from which they took to the air. The next morning only a plugged hole was visible, the workers having dismantled the shelf during the night. Mr. James Zetek observed a somewhat similar construction during a flight of *C. niger* Snyder from the base of a tree in Ancon, Canal Zone, on August 26, 1923.

It is extremely difficult to analyze such behavior in terms of responses to simple stimuli. Although our ignorance is great, one must assume responses to intricate social stimuli. Anthropomorphic explanations, however, do not assist our understanding.

NESTING BEHAVIOR OF THE TERMITIDAE

The Termitidae are morphologically and socially the most specialized of the termites and have doubtless evolved from a rhinotermitid stock. The abundance of nest types are too numerous to describe in this report and only a few of the more outstanding and significant examples will be mentioned.

Many nests of the Termitidae are not more elaborate than the simplest nests of the Rhinotermitidae. In fact, some nests seem even less complex. The author dug into a subterranean nest of *Syntermes snyderi* Emerson in the rain-forest of British Guiana (Fig. 2) and found galleries extending

FIG. 2. Subterranean excavated nest of *Syntermes snyderi*.
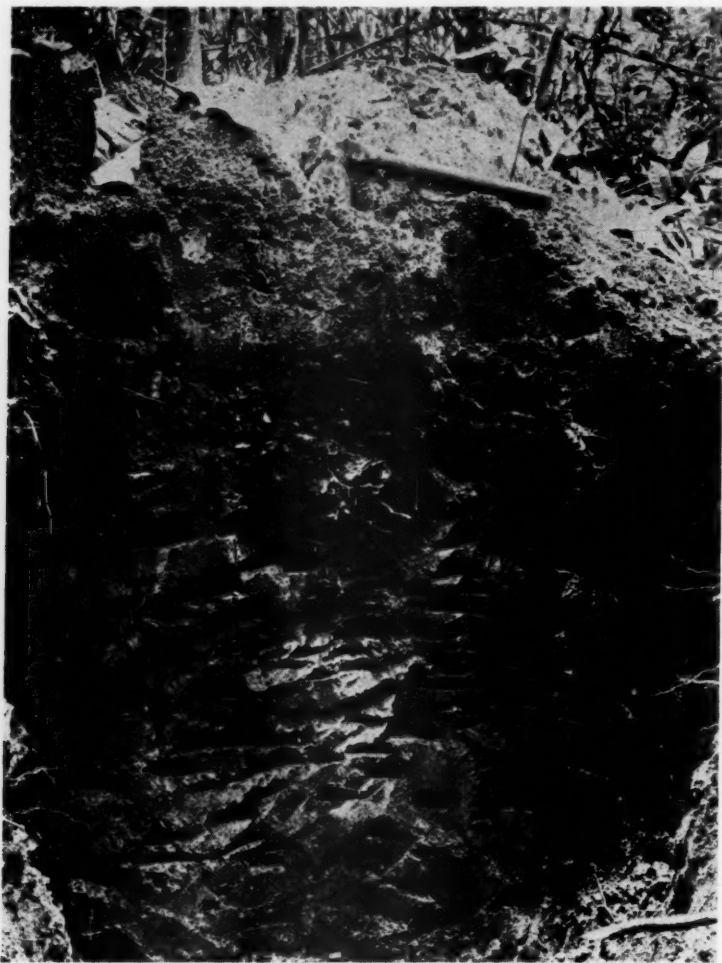
below the surface to a depth of about four feet and covering a horizontal circular area with a diameter of about twelve feet. The galleries were large and seemed to be simple excavations in the sandy-clay soil, although there were small lumps lining the galleries in places that might have been excretions of the termites. The excavated dirt was deposited on the surface in

loose piles above the nest. No covered tunnels were constructed on the surface, the termites moving in exposed trails. They cut out pieces of dead leaves which served as their food. Leaf fragments about one centimeter in diameter were stored in some compartments of the nest.

The humidity and consistency of the material composing the walls of the excavated galleries must be fairly constant in such a nest. The excavating termites would seem to be reacting to spatial factors as well as to strains in the supporting walls, rather than to humidity or differentiation of material as in the case of *Kalotermes flavicollis* described in the preceding pages.

NEST MATERIALS

Materials composing the nests of termitids (see Hegh, 1922) are similar to those already described, but one often finds a given group specializing in the use of certain substances. Most of the species use particles of dirt or sand. The nest of *Anoplotermes (A.) silvestrii* Emerson in British Guiana was of such extreme hardness that sparks flew from the hatchet when the nest was opened. In laboratory colonies, no abdominal excretion was observed during the nest building activities. Each particle of dirt was moistened only with a salivary secretion as the worker placed it in position. Laboratory colonies of *Microcerotermes arboreus* Emerson, however, revealed the workers placing pieces of dirt moistened with saliva in place and then turning and excreting a drop of thick dark fluid upon the newly inserted particle. *Crepititermes verruculosus* Emerson exhibited still different actions. Practically all the building observed in the laboratory was constructed through the use of abdominal excretions of thick dark fluid. The intestines of the workers seemed to be filled with this muddy material. They were sometimes observed to bring pieces of material for building, but no salivary secretion was seen nor did they work the material into place in the manner so characteristic of most termites.

On the other hand, wood derivatives are used almost exclusively by the majority of the species of *Nasutitermes, s. str.* (Fig. 3), a tropicopolitan group of termites composed of a large number of species. These termites can build typical nests in such places as the branches of standing dead trees which have been killed by the rise of dammed waters in Gatun Lake during the construction of the Panama Canal. Such nesting sites are not available for species dependent upon dirt in the construction of their nests.

Beaumont (Dudley, 1889, p. 91) described the construction activity of a species of Panamanian termite (either *N. corniger* (Motschulsky) or *N. ephratae* (Holmgren). The behavior is essentially similar to that described for *Microcerotermes arboreus* except that particles of wood or carton are used instead of dirt. Bugnion (1927, p. 18) also gives a fine detailed account of similar behavior of *Nasutitermes (= Eutermes) ceylonicus* (Holmgren) which uses both wood, sand and abdominal excretions in its construction. An

interesting variation was observed by the author while watching captive
colonies of *Nasutitermes guayanae* (Holmgren) in British Guiana. Instead
of placing the piece of material in its position with saliva and then excreting

FIG. 3. New cells in process of construction during the
enlargement of the nest of *Nasutitermes guayanae*.

abdominal fluid, the termite invariably excreted the abdominal substance
first, and then turned and worked the piece of building material into place
with its mandibles.

STRUCTURES

The structures vary considerably in form and function (see Hegh, 1922),
thus indicating a wide variety of stimuli affecting the behavior pattern. Cov-
ered tunnels may lead out from the nest. These are built along odor trails
followed by the termites at times of high humidity. One of these covered
tunnels built by *N. guayanae* led from a nest thirty feet up in a palm tree,
down some vine stems to the ground, and around by a sandy clearing in the

forest to a small dead tree. In all, the distance was 162 feet, although the dead tree was only 35 feet in a straight line from the palm tree.

The covered tunnels may lead down into the ground where the excavations are lined with carton (materials cemented by saliva or excrement). Covered tunnels on the walls of Chilibrillo Cave, Panama, made by *N. corniger*, were estimated to be about twenty feet below the surface of the ground.

William Beebe observed *Macrotermes carbonarius* (Hagan) at Penang, Malaya, walking in open trails on carton roadways which the termites constructed over rough ground (See Emerson, 1937a, p. 247). I assume these roads to be a response to mechanical factors.

Termites will use the same materials used in the construction of their nest or tunnels for burying foreign insects introduced into their colony. Dudley (1889) has figured this action in *Nasutitermes* and the author has witnessed it many times following the attack upon an introduced foreign termite or termitophile.

The size of the nest is quite often fairly characteristic of the species. For example the nests of *N. pilifrons* (Holmgren) were quite often much larger than those of *N. corniger* or *N. ephratae* in Panama. Likewise in British Guiana, the nests of *N. surinamensis* (Holmgren) were typically larger than those of *N. guayanae, N. costalis,* or *N. ephratae* and, in turn, these were larger than the nests of *N. gaigei* Emerson. The huge dirt nests of *N. pyriformis* (Froggatt) reaching a height of 18 feet would seem to be characteristic of the species (Froggatt, 1905). The size of the nest may be proportional to colony size and reproductive capacity. The number of individuals in one nest (Emerson, 1937a, p. 247) of *N. surinamensis* was estimated quite carefully to be three million in round numbers. The nest measured six feet in height and three and one-half in greatest diameter. The queen from this nest was 24 mm. long and 8 mm. wide. She laid 2938 eggs in 18 hours. A small nest of *Microcerotermes arboreus* in British Guiana seemed small enough to count the entire colony (excepting foragers). It measured 6 in. long, 2 in. wide and 2 in. thick. The volume was approximately 110 cu. cm. There were 5876 termites and 2109 eggs in the nest. 4006 of the termites were mature and 1870 were nymphs. The mature individuals were composed of 1 queen, 1 king, 114 soldiers, and 3890 workers divided into 2624 large light-headed types, 939 small dark-headed types and 327 intermediates. Two larger nests of this same species contained about 250,000 eggs and 300,000 eggs respectively. A queen measuring 21 mm. in length laid 1680 eggs in 24 hours. The highest rate of oviposition which I have measured was 357 eggs in one hour in the case of a queen of *Anoplotermes silvestrii* which measured 50 mm. in length. These tropical queens continue to lay eggs steadily without much variation during diurnal or seasonal cycles and are doubtless often quite old. Through consideration of nests in Africa known to be at least

40 or 50 years old and each occupied by a first form queen, I think such an age for some of the reproductive castes is not impossible.

Enlargement of the nest may indicate some of the stimuli to which the workers respond. In the case of *Nasutitermes guayanae* (Fig. 3) a hole in
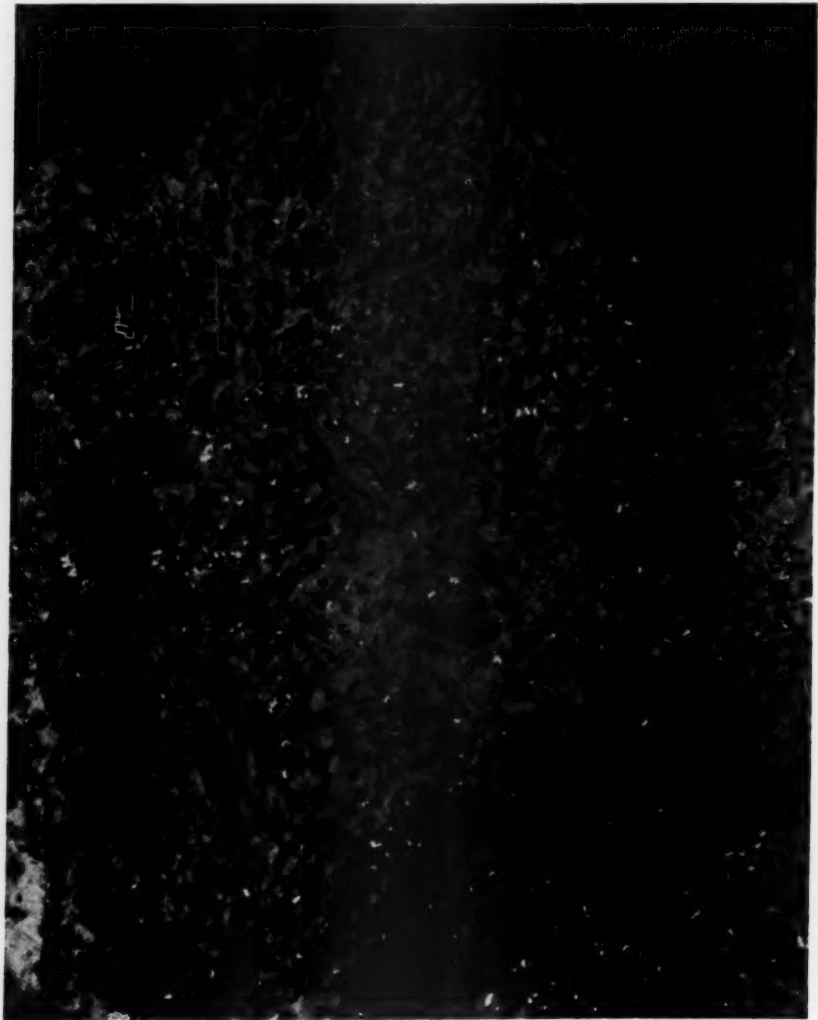
FIG. 4. Vertical section of a nest of *Nasutitermes costalis* showing the thick walls in the vicinity of the royal cell.

the exterior of the nest is made and a new cell is built over the opening. Workers build the walls on all sides until they meet at the top. *Constrictotermes cavifrons* (Holmgren) enlarges its nest by roofing the area between parallel surface ridges (Fig. 14). The point of junction between the walls is perfectly even and seems to be explained only in terms of subtle sensitivity to spatial relations. The subsequent thickening of the walls of the cells takes place below the surface. The walls in the vicinity of the royal cell are greatly thickened in the nests of many species of termites (Fig. 4) evidently stimu-

lated by the presence of the queen. Grassé (1937) gives an interesting and detailed account of the organization of the nest of *Macrotermes (Bellicosi-termes) natalensis* including consideration of the royal cell.

Holdaway (1933) gives interesting data upon the chemical differences in materials composing the parts of the mound nests of *Nasutitermes* (= *Eu-termes) exitiosus* (Hill). An analysis of the inorganic material shows that the outer wall averages 64 per cent, the inner wall 15 per cent, and the "nursery" 11 per cent. There seems little doubt that social and environmental factors influence the use of materials in the same nest.

FIG. 5. Mound nest of *Amitermes medius* Banks. Aguadulce, Panama.

By far the most astounding structural detail in the construction of nest walls is to be found in the subterranean nests of the various species of the African genus *Apicotermes*. Careful descriptions and figures of these nests have been published (Desneux 1918; Hegh 1922, pp. 385-394, 712; Sjöstedt 1923, 1926, Taf. 13; Reichensperger 1923). The determination of the known species is to be found in Sjöstedt (1926, p. 153). The simplest of these nests has external walls perforated by tiny pores or channels too small for the termite to walk through and probably functioning as ventilation pores. The next most complex nest has the external openings of the pores emerging into small pits or holes considerably wider than the pores, and the most complex nests have circular galleries within the walls connected to the outside by small pores and to the inside by small pores of approximately equal diameter. In the latter case, it would seem difficult not to assume that the pits or holes of the second type of nest had evolved into the circular galleries of the third type. Such behavior evolution would seem to present a sequence which reminds one of the ascon, sycon and leucon types of canal systems in the sponges. The nests of *Apicotermes* also illustrate most clearly the inherent nature of the hereditary influences upon the behavior which are generic in character rather than distinctive of species alone. Of course we might expect to find certain types of behavior characteristic of larger groups than genera, and such is the case. The finest example of distinctive construction behavior characteristic of an entire subfamily (Macrotermitinae) is discussed later.

Kinsey (1936, pp. 8, 56, 57) reviews current concepts of higher taxonomic categories. Among others, the concept that genera, subfamilies and families are arbitrary groupings merely for the convenience of the taxonomist and

without objective reality has often been stated. The correlation of many morphological characteristics together with behavioristic, physiological, ecological and geographical characteristics as seen in the genera, subfamilies and families of termites has convinced the author that the groups of species are indicative of a relationship which may be scientifically symbolized in the names of the higher categories which thus rest upon sound objective evidence with statistical significance of correlation.

As has already been pointed out, food is sometimes stored in the cells of the nests of *Hodotermes* and *Syntermes*. Food storage may involve construction activity also. In the nest of *Constrictotermes cavifrons* (Fig. 14) the basal hanging portion is composed of a dark pasty material which I interpret to be stored food. It is possible, however, that this is segregated excrement. In any case, the material has sufficient nutrient value to be used by a large number of other insects including tineid caterpillars probably belonging to the genus *Amydria* or *Exoncotis* (det. W. T. Forbes), larvae of an acanthocerid of the genus *Acanthocerus*, elaterid larvae, larvae of the sciarid genus *Sciara*, and finally another species of termite, *Termes (= Mirotermes) inquilinus* (Emerson). *T. inquilinus* has never been found in any other place and I am confident that it is confined to the nests of *C. cavifrons*. Its galleries are separated from those of the host termite and are lined with carton of its own construction, but the nesting activities largely consist of excavations in the stored organic material deposited by the host termite. If the two species come together when the nest is opened, a violent battle ensues. Although the nests of the genus *Termes* are not as definitive as those of most species of *Nasutitermes*, it seems safe to assume that this particular species of *Termes* has undergone degenerative evolution of the nesting behavior in association with its social semi-parasitism. The closest related species, *Termes fur* (Silvestri), seems to have the same relationship to *Constrictotermes cyphergaster* (Silvestri) (Silvestri 1903, p. 128). These cases remind one of the evolutionary degeneration of the nesting behavior among the parasitic birds and the genus *Psithyrus* of the bumble bees.

Kemner (1929) interprets the existence of carton nodules in the nests of *Microcerotermes depokensis* Kemner as food storage activity. Similar nodules were observed in nests of *Nasutitermes pilifrons* during my studies of Panamanian termites, but I am not sure of their function.

Probably the most remarkable construction activities associated with nutrition are to be found in the fungus gardens of all species of the subfamily Macrotermitinae. The excrement of the termites or finely pulverized plant material (see Grassé, 1937) is built into elaborate convoluted structures so organized as to give a maximum surface for the growth of the fungus (Wheeler 1907; Sjöstedt 1907; Hegh 1922; Bugnion 1927). The gardens are quite distinct from the rest of the nest, which is constructed in quite a different manner. They present a picture of complex reactions to complex

stimuli. Fungus-growing behavior is confined to this subfamily of termites. Examples of nest-building behavior patterns characteristic of higher taxonomic categories of birds are given by Chapin (1917).

CASTES INVOLVED IN NEST CONSTRUCTION

The nests of the primitive Kalotermitidae are excavated or constructed by the nymphs of the soldiers and reproductive castes except for the original cell of the colonizing pair. It is probable that the Mastotermitidae follow

FIG. 6. Mounds of *Amitermes vitiosus* (?) Hill between Camooweal, Queensland, and Newcastle Waters, Northern Territory. Photograph through the courtesy of G. F. Hill.

the same rule. The situation among the Hodotermitidae is more obscure because the exact status of the darkly pigmented, eyed "worker" has not been definitely established. Among the Rhinotermitidae and Termitidae, the adult sterile worker has become differentiated through neoteinic evolution from the soldier nymph (Emerson, 1926, 1935; Hare, 1934). However, it is quite common to find smaller worker-like forms, fully pigmented and with the abdomens containing the same materials as those found in the adult workers. These individuals seem to be nymphs of workers or soldiers and their behavior is the same as that of the adult workers as far as is known (Emerson 1926). It is thus probable that the worker-like nymphs of the soldiers have the same complex behavior patterns as the workers, and function in the construction and nutrient activities. Mature soldiers, however, never seem to assist in nest building. Snyder (1920, p. 190) states that the nasute soldier uses the fluid exuded from the beak in making shelter tubes, but I am convinced that this statement is an error. It has not been demonstrated that the nymphs of the reproductive castes of the Rhinotermitidae or Termitidae ever take an active part in gathering much food or constructing

the elaborate nests. The construction of the original cell in wood or dirt by the colonizing pair, however, indicates that nesting behavior has not been wholly inhibited in the reproductive castes.

Spencer (1893) attempted to explain the differences between the behavior of the reproductive caste and the worker in the Hymenoptera as a loss of instinct on the part of the reproductive caste, the primitive species having the instincts before caste divergence took place. Holmes (1911) points out

FIG. 7. East face of mounds of *Amitermes meridionalis*.
Photograph through the courtesy of G. F. Hill.

the weakness of this contention, which is further demonstrated in the behavior evolution occurring long after the establishment of the adult sterile worker caste among the termites.

ECOLOGICAL FUNCTIONS OF THE NEST

The nest would seem to be of value to the termites as a means of controlling certain variables in the environment or for allowing sufficient elasticity of conditions to enable the insects to avoid certain environmental extremes. In order to test the variation in temperature within nests in relation to variations in the environment, two nests of *Nasutitermes corniger* on Barro Colorado Island were chosen. One was located in a clearing on a small stump, the base in contact with the ground and the top two feet from the ground. The stump was under a banana tree and was forty feet from the edge of the forest. The greatest diameter of the nest was one foot. A short thermometer (4 in.) was placed in a hole stoppered by a cork. The hole was about 1 inch wide and the bulb of the thermometer was 5½ inches from the surface. The other nest was attached to a small vine in the forest about twenty feet from the edge of the clearing. The forest roof was about fifty feet high. The bottom of the nest was 1½ feet from the ground. The nest was 2 feet high and 1½ feet in greatest diameter. A hole about 1 inch wide was dug into the nest so that the bulb of the thermometer (matched with the

TABLE 1. TEMPERATURE AND LIGHT MEASUREMENTS THROUGH A DAILY CYCLE IN THE ENVIRONMENT AND IN CLEARING AND FOREST NESTS OF *Nasutitermes corniger* IN PANAMA.

Time	CLEARING				FOREST				Remarks
	Nest Temp. °F.	Shade Temp. °F.	F. C. Light on Nest	F. C. Light in Sun	Nest Temp. °F.	Shade Temp. °F.	F. C. Light on Nest	F. C. light in Sun Fleck	
10 A.M.	79.0	83.5	1300	10500	80.5	82.0	25	200	Sunny
11 A.M.	86.0	86.0	11500	11500	81.0	81.0	20	5000	Sunny
12 M.	87.0	85.0	8500	8500	81.5	79.5	30	5500	Sunny
1 P.M.	90.0	86.0	9500	9500	82.5	79.5	10	30	Partly cloudy
2 P.M.	92.0	79.5	800	800	83.0	77.5	¼	—	Cloudy
3 P.M.	92.0	79.5	950	950	83.0	77.0	5	—	Cloudy
4 P.M.	91.0	80.0	195	195	83.0	78.0	0	—	Light rain
5 P.M.	91.0	79.0	160	160	83.0	78.0	0	—	Light rain
6 P.M.	89.0	77.5	50	50	83.0	78.0	0	—	Light rain
7 P.M.	88.5	77.5	0	—	82.5	77.0	0	—	Rain stopped
8 P.M.	87.0	74.5	0	—	82.5	74.5	0	—	Stars out
9 P.M.	84.5	74.5	0	—	82.5	74.0	0	—	Stars out
10 P.M.	83.5	74.0	0	—	81.0	74.0	0	—	Stars out
11 P.M.	82.0	74.0	0	—	80.5	74.0	0	—	Stars out
12 P.M.	82.0	74.0	0	—	80.5	74.0	0	—	Stars out
1 A.M.	82.0	73.5	0	—	81.0	74.0	0	—	Stars out
2 A.M.	81.0	74.5	0	—	79.0	74.8	0	—	Cloudy
3 A.M.	81.0	74.5	0	—	79.0	75.0	0	—	Stars out
4 A.M.	80.5	74.5	0	—	78.5	75.0	0	—	Stars out
5 A.M.	79.0	74.5	0	—	78.5	75.0	0	—	Stars out
6 A.M.	79.5	75.8	5	5	78.5	75.0	0	—	Cloudy
7 A.M.	80.0	77.0	450	450	78.5	76.0	10	—	Cloudy
8 A.M.	80.5	78.0	600	1800	78.0	77.5	50	300	Sunny
9 A.M.	81.0	79.0	1100	1200	78.5	77.0	15	15	Cloudy
10 A.M.	82.0	80.5	1600	1650	78.5	78.0	20	25	Cloudy
11 A.M.	83.0	83.0	2500	3000	79.0	79.0	25	35	Dim sun

thermometer in the clearing nest) was 6½ inches from the surface and the hole was stoppered. Measurements (Table 1) were taken approximately on the hour on September 2d and 3d, 1935, for a period of over 24 hours. Light readings (in foot candles) were taken by means of a Weston illuminometer. In general the measurement of illumination in the sun in the clearing showed little difference from that on the nest. A light rain fell intermittently from 2.30 to 7.00 P.M. and doubtless influenced the temperature and illumination records.

One concludes from these measurements (Table 1) that (1) the direct sun rays on the nest raise the internal temperature above the shade temperature of the surroundings, and (2) that the temperatures follow the daily rhythm of the external temperatures, but lag behind the rising and falling external temperatures and do not reach the extremes found outside the nest. Of course, the sun temperatures outside the nest which reached maxima above 120°F. (the limit of the thermometers available) were far in excess of any internal nest temperature, and the nest temperatures measured above the maximum shade temperatures were doubtless due to the direct rays of the sun.

It is thus possible to say that the nest structure partially protects the

termites from the temperature extremes found outside of the nest. Cowles
(1930) measured external and internal nest temperatures in the nests of
Trinervitermes trinerviformis in Natal and his table shows the same tend-
ency in these mound nests. Subterranean nests probably follow the tem-
perature cycles of the surrounding soil very closely and this feature may be
considered one advantage of such a habitat. Although it is possible that
there is some migration of termite workers and soldiers influenced by tem-

FIG. 8. South end of mounds of *Amitermes meridionalis.*
Photograph through the courtesy of G. F. Hill.

perature variations within the nest (Holdaway, 1935) and between the nest
and the ground, the queen is of necessity usually confined to the royal cell and
the young nymphs are seldom found far from the center of the nest.

Of probably greater importance than temperature is the control of hu-
midity within the nest as compared to the extremes to be found in the ex-
ternal air. No measurements of nest humidities have been made, but it is
safe to assume that the occupied nests of the Rhinotermitidae and Termitidae
have almost a saturated air humidity (See Cowles, 1930, p. 23). The
reaction of these termites to humidity gradients (Williams 1934; Emerson,
unpublished experiments) indicates that they move away from dry air toward
saturated air and that they die from even a brief exposure to dry atmosphere.
Species of the Kalotermitidae often show more toleration to dry atmosphere
and also often do not move from dry air to saturated air when exposed to
humidity gradients. It is this dependence upon saturated or nearly saturated
humidity that is probably the most important reason why the rhinotermitids

and termitids are typically soil termites and, when above the surface of the soil, they typically construct nests and tunnels which maintain humid conditions not very different from the subterranean habitat. Slight differences in the moisture requirements between *Reticulitermes hesperus* Banks and *R. tibialis*

FIG. 9. Rain-shedding dirt-carton nest of *Amitermes excellens*. A wood-carton nest of *Nasutitermes guayanae* is visible on the right side of the trunk.

Banks demonstrated by Williams (1934) make it reasonable to suppose that such differences may often determine the ecological distribution of the species. Even the desert termites, however, so control the humidity of the air surrounding them that they live in an atmosphere close to saturation. The case is different in the Kalotermitidae, however, and the ability of *Cryptotermes*, for example, to live in the wood of dry furniture is doubtless linked with a greater toleration to dry atmosphere than is found in the species of Rhinotermitidae and Termitidae.

Other factors that may be of some importance to termites are the oxygen necessities and the elimination of carbon dioxide. Williams (1934) reports positive experiments upon these factors. The ventilation pores in the nests of *Apicotermes* may function for the exchange of gases. It may well be that the elimination of carbon dioxide may determine the site of the nest to some extent. Soil heavily soaked in water or with the surface flooded would certainly not offer a favorable site for a termite nest and the tendency to construct mounds and arboreal nests may enable termites to live in otherwise unfavorable localities.

The termite literature abounds in references to the avoidance of light. The only definite orientation with response to light of which I am aware among termites is the photopositive reaction of the winged imagoes during the first part of the colonizing flight. I have myself reported (Emerson 1929) a "negative phototropism" of the imagoes before the flight starts and after it is finished, but more accurate experimentation indicates that the pho-

topositive reaction is only present for a short time and the insect is neutral to light at other times. This neutrality does not apply to heat and to increased evaporation, however, and the actions usually interpreted as negative responses are probably the result of these other factors which are so often
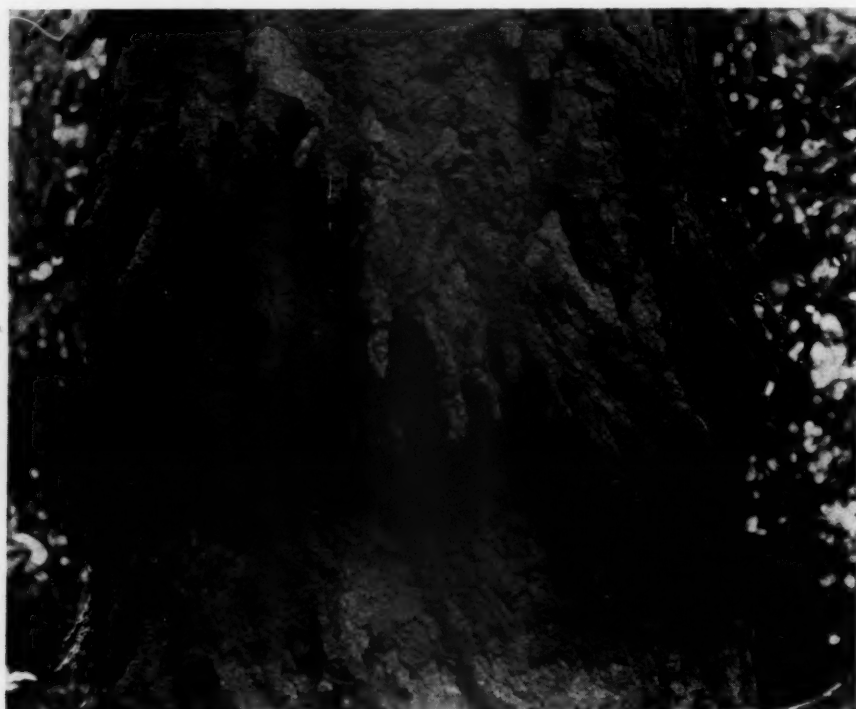
FIG. 10. Detail of rain-shedding projections of nest of *Amitermes excellens.*

closely associated with increase in the intensity of light. I should consequently not interpret the construction of nests or tunnels as the result of photonegative behavior.

Another factor emphasized in the literature, particularly by Bugnion (1927), is the construction of the nests for the protection of the inhabitants from predatory enemies. It is certainly true that exposed termites form ready prey for wasps, ants, spiders, lizards, and other predators. Ants in particular have doubtless been enemies of termites for many ages and some species prey only upon termites (Wheeler 1936). Experiments as yet unpublished indicate the ability of the soldiers to combat these enemies in comparison with the defensive ability of the workers. The evolution of the soldier caste has doubtless been guided by the selection of efficient means of defense against predators and it is quite conceivable that the nest-building patterns have also been selected because of their value in protecting the colony from attack. I have never observed a direct influence of the presence of predators upon construction which cannot better be explained as a response to other factors, however, and I am of the opinion that any such direct re-

sponse to ants as that postulated by Bugnion (1927, pp. 14, 30) needs critical verification. A few predators are especially adapted to overcome the protection the nest affords. The modified forefeet of the spiny anteater, pangolin, aard vark, and New World anteaters enable these animals to invade the hard nests of termites. The cylindrical sticky tongues of these phylogenetically diverse mammals are astonishingly efficient in penetrating the complex system of cells in the termite nest. The prehensile tail, found in the tamandua, silky anteater, and some pangolins, enables these predators to reach the arboreal nests. The remarkable adjustments of these specialized termitophagous mammals only serve to emphasize the value of the nests as protection from general predators and indicate how strong the selection pressure was to influence the evolution of such striking convergent adaptations.

Not only is the nest a protection against animal predators, but it is also a protection from harmful fungi. Laboratory colonies removed from nests often succumb to molds which seem to be effectively controlled under natural conditions.

SELECTION OF THE NESTING SITE

One might suppose that the selection of the nesting site involved no more behavior response than is found in seeds scattered by the wind. It is true that the flying termites scatter in all directions and a very large proportion alight in unfavorable locations. I have seen thousands entrapped in the surface of a river where fish were rapidly devouring them. I have seen thousands die of heat and evaporation on the hot sands of dunes. I have seen paired couples entering crevices in a wharf which was soon to be inundated by a rising tide. Certainly the mortality is high during the colonizing flight. On the other hand, the colonizing pair in *Termes inquilinus* and *T. fur* would seem to select the nests of *Constrictotermes cavifrons* and *C. cyphergaster* respectively for their nesting site and there are other indications that the imagoes are not wholly subject to chance. There is strong evidence that considerable powers of selection are manifested, not so much by the colonizing pair as by the workers after the colony has developed. The migration of an entire colony of *Nasutitermes costalis* including the royal couple and many termitophiles has been reported (Emerson, 1929). The process of moving the nesting site will rarely be seen by human eyes, but migrations must be assumed when nests are found in locations where the royal pair could not have excavated their original cell. Such is the case for every nest of *Constrictotermes cavifrons* seen in the British Guiana forest (Fig. 14). These nests were invariably found on living trees with smooth bark, and in nine out of ten cases the tree slanted at an angle to the ground. The living bark was not invaded by the termites. The evidence seems convincing that all these nests were established through the migration of the entire colony. The uniformity of the nesting site in this species indicates behavior reactions

of which we know practically nothing. How blind, rather small insects can select a tree with smooth bark rather than rough, the under side of a slanting surface rather than the upper, and then, after at least preliminary construction by hundreds of individuals, stimulate the entire colony including the grossly physogastric queen to move to the new site, is difficult to analyze. It is not surprising that uncritical commentators fall back upon anthropomorphic explanations of such facts.

Especially in arboreal nests, height above the ground may be characteristic of the species or genus. Of the nests which I have studied in the New World, *Nasutitermes costalis, N. ephratae, N. surinamensis, N. wheeleri, N. acajutlae, N. corniger, N. pilifrons, N. guayanae, N. similis, N. columbicus, Constrictotermes cavifrons, Anoplotermes (Speculitermes) arboreus, Amitermes excellens* and *Microcerotermes arboreus* build at varying heights from the ground. The last four species build dirt carton nests and the others build of wood carton. Other species seem to be limited to sites at most only a few feet above the ground, such as *Anoplotermes silvestrii, A. banksi, A. brevipilus* and various species of *Termes* and *Armitermes*. Every gradation from these sites to subterranean locations may be found, but the range for each species seems to be fairly characteristic, although there may be considerable variation within each species.

Nests may be built quite rapidly. A nest of *Amitermes excellens* Silvestri was constructed about 50 feet from the ground on a tree near the Kartabo laboratory between September 15, 1919, and June 1, 1920. This nest was about 3 feet long, 1 foot wide and ½ foot thick. A colony of stingless bees had partly occupied the interior. I assume that the colony migrated to a new site in this case. Nests enlarged in proportion to the growth of the colony would doubtless grow more slowly.

NEST DIVERGENCE WITHIN A GENUS

It has often been observed that adaptive modifications are more conspicuous as one ascends in the ranking of the animal group. Adaptations between families are more obvious than between genera, and adaptations between genera are more obvious than between species of the same genus. One explanation of this difference in different categories may be that genera arise through further speciation of adapted species, while less adapted species may not survive through the ages of competition. Striking adaptive divergence probably takes a long time under fairly strong selection pressure, while speciation mechanisms may operate with slight selection (Wright, 1932, p. 363). If the mechanisms of evolution are operating to produce adaptive behavior in the same way that they operate to produce adaptive physiological interaction and structural growth, we may expect to find this rule illustrated in the nesting behavior of termites.

The general outline of family differences in nests has already been pre-

sented. Many genera show similar nesting tendencies between various species, notably the dirt carton nests of *Microcerotermes*, the wood carton arboreal nests of most species of *Nasutitermes, s. str.* (Figs. 3, 4, 9), the mushroom-shaped nests of *Cubitermes* (Fig. 11), and the perforated nests of *Apicotermes*.

It is also possible to show striking divergence between the nests of species of the same genus, notably in the genera *Nasutitermes, Anoplotermes*, and

Fic. 11. Mushroom-shaped dirt-carton nest of *Cubitermes loubetsiensis* Sjöstedt, Medje, Belgian Congo. The cap with peripheral projections sheds rain from the stem. The height measured 44 centimeters. The vertical section shows the connecting holes between the cells and the queen in the middle just above the narrow part of the stem. Photographed by Herbert Lang.

Apicotermes. I have selected the genus *Amitermes* as the best example known to me which illustrates such divergence as well as striking adaptive nest modifications.

Amitermes is a genus found in every zoogeographical realm, but in general it is found in the tropics and only in the warmer portions of the temperate realms. As a genus, it seems particularly adjusted to dry regions, many more species being found in such regions as the southwestern semi-deserts of the United States than in the rain-forests of the tropics.

The majority of the species do not build definitive nests above the ground which lend themselves to photography. Examples of such inconspicuous nests are those of *A. beaumonti* Banks in Panama, *A. wheeleri* (Desneux) in Texas, and *A. santschii* Silvestri in north Africa.

A number of species, particularly in Australia, build mounds above the ground which may be conspicuous features of the landscape (Figs. 5, 6). Illustrations of such nests of *Amitermes* are to be found in Hill (1922, 1922a, 1935), Froggatt (1905), Mjöberg (1920), Hegh (1922), Snyder and Zetek (1934), Emerson (1937a). It will be noted upon examination of these various photographs that there is a fair amount of variation in the shapes of the nests within a given species, but it is also obvious that characteristic distinction between the different species exists and in several instances the species may be easily recognized by means of the nest alone.

From many viewpoints, the most remarkable nest known is that of *A. meridionalis* (Froggatt). This nest is the famous "magnetic" nest found in north Australia (Figs. 7, 8) which is figured by Froggatt (1905), Hegh (1922), Hill (1922, 1935), and Emerson (1937a). Hill (1935) questions the determinations of the nests described and figured by Saville-Kent (1897, 1897a) and Mjöberg (1920). The largest of the "meridian" nests are about 12 feet high with a north-south length of about 10 feet and an east-west width of about 3½ feet at the base in the middle. Hill (1935) gives the most complete and accurate account of the geographical and ecological distribution, the shape and orientation of the nest, and a discussion of the theories to account for the peculiar orientation. Hill states (private correspondence):

I have thought that the probable reasons for the mounds being built with the long axis approximately north and south is to obtain the maximum total amount of solar radiation during the winter months, and the minimum during the heat of the day in summer.

It would seem to me that the explanation probably will ultimately be found in the control of temperature, although theories placing emphasis upon humidity and wind have already been proposed. Not only is the explanation of the adaptive value of such a nest important, but a knowledge of the factors to which the termites are reacting directly would add much to our concept of nest evolution.

Andrews (1927) and Dreyer and Park (1932) discuss ant nests of the genus *Formica* which are oriented with reference to light and give measurements of light and temperature. These ant nests have their broadest face toward the south and the most direct rays of the sun. The difference in the orientation of the nests of *A. meridionalis* may very likely be owing to their tropical location and possibly to the greater extremes of temperature to which they are subjected.

In sharp contrast to the mound nests of the more arid savannahs, *A. excellens* constructs nests on the sides of surrounding trees in the rain-forest of British Guiana. Galleries covered the entire trunk of a dead tree in an old clearing near the Kartabo laboratory (Figs. 9, 10). The tree was covered to a depth of about 8 inches and to a height of about 45 feet. The material was a sandy-dirt carton which easily crumbled in the hand. The exterior

was covered by numerous finger-like projections extending downward and outward. Upon breaking these projections they proved to be hollow and were always occupied by a few termites. The function seems to be for the shedding of rain water during heavy tropical showers. In this particular

FIG. 12. Rain-shedding dirt-carton nest of *Cubitermes subarquatus* on a tree at Medje, Belgian Congo, composed of a series of caps with peripheral projections. Photographed by Herbert Lang.

FIG. 13. Nest and rain-shedding, chevron-shaped structures of *Procubitermes niapuensis* on a tree at Niapu, Belgian Congo. Photographed by Herbert Lang.

locality the annual rain fall was around 110 inches. Heavy rain fall (5 to 8 inches) of short duration was not uncommon.

When these structures are first started on the side of a tree, a long vertical covered gallery is built on the trunk, and side branches are built in a peculiar parallel arrangement inclined downward on the tree at an angle of about 45° to form a "herring bone pattern" (Emerson, 1937a, p. 246). The function of this construction is also probably the efficient shedding of rain which descends the tree trunk.

CONVERGENT EVOLUTION WITHIN A SIMILAR HABITAT

The adaptive significance of a modification is more convincing if it is possible to show that organisms from stocks not possessing the modification have separately evolved a similar adjustment when subjected to natural selection within a similar habitat. The function of the finger-like projections on the nest of *Amitermes excellens* becomes more clear if similar nest structures appear in unrelated termites typically found in or near rain-forests. Convergence of rain-shedding structures may be demonstrated in three different subfamilies of the Termitidae including the Amitermitinae already discussed. Without doubt these subfamilies had no common ancestor from which they could have inherited such a pattern.

The Termitinae include several African genera which can be arranged in a series possibly illustrating an evolutionary sequence. *Cubitermes* often constructs a unique mushroom-shaped nest (Fig. 11), the specific variations of which have been well illustrated by Sjöstedt (1913), Hegh (1922), and Emerson (1928). These nests show definite generic similarity but at the same time show specific differences. The majority are capped by an umbrella-like structure, convex on top and projecting outward at the periphery in such a way as to shed rain from the top of the nest. Finger-like projections, quite similar to those described on the exterior of the nest of *Amitermes excellens*, often extend around the edge of the cap. The nest of *Cubitermes subarquatus* Sjöstedt (Fig. 12), found in the Congo rain-forest, deviates from the mushroom-shaped form found in more open country by appearing to be a succession of caps, one above the other. This nest type might easily have evolved from the mushroom type. The remarkable nest (Fig. 13) of a species from the Congo rain-forest, *Procubitermes niapuensis* Emerson, belongs to a closely related genus. The termites build a series of hollow, chevron-shaped, dirt-carton structures extending for some distance above the nest proper on the side of the tree trunk. Mr. Herbert Lang, who examined and photographed the nest, is of the opinion that the ridges function for the shedding of rain (Emerson 1928).

In the rain-forest of British Guiana, still another nest exhibits rain-shedding modifications (Fig. 14). The species is *Constrictotermes cavifrons* belonging to the Nasutitermitinae. The entire structure sometimes reaches a length of about 3 feet. It is attached for most of its length to the side of a smooth-barked live tree. A discussion of other features of this nest is to be found in the preceding pages. Pertinent to our present consideration is the series of solid, sharp carton ridges which extend over the surface of the nest and continue downward at an angle along the tree trunk at the sides of the nest. These ridges are also built some distance above the nest and form a series of chevron-shaped structures which remind one of similar structures in the nest of *Procubitermes niapuensis* (Fig. 13). In the case of the nest of *C. cavifrons*, however, the ridges are more numerous, are sharp and solid,

and are built over the surface of the nest. The surface of the bark is cleaned of lichens and similar outgrowths between the ridges, and an open passage-way is left above the nest which allows ease of travel up the tree. I have observed the nest during a heavy shower and there is no question that the

FIG. 14. Profile and detail of edge of nests of *Constrictotermes cavifrons* on smooth-barked slanting trees at Kartabo, British Guiana. Sharp, solid, rain-shedding ridges extend above the nest on the tree trunk as well as over the surface of the nest and down the sides of the trunk. The termites have bridged over the ridges as they enlarged the nest (upper right). The hanging basal part of the nest (lower left) is composed of stored food and is occupied by the semi-parasitic termite, *Termes inquilinus*.

ridges deflect the sheet of water descending the trunk of the tree in such a manner as to keep the nest relatively dry and moistened only by the drops which fall directly upon it. Hingston (1932) describes this nest and arrives at the conclusion that the ridges "shoot the water forward and outward clear of the nest." My observations did not indicate that the water was "shot" outward, but that the stream was deflected to the side and ran down the trunk without wetting the nest. Hingston also describes an experiment in which he cut 18 ridges above the nest, allowing the water to run into the nest. He

states that the water moistened and softened the earth carton of which the
nest is composed. In the fourth week following the injury to the ridges, the
termites started to repair and replace the ridges and had completed eight
during the sixth week when the observations ceased. This experiment of
Hington's is most interesting because it indicates that the termites may react
to the percolation of the rain-water into their nest.

DISCUSSION

Because the insects in the experiment outlined above have successfully
met an emergency, Hingston classifies this behavior as intelligence (also see
Imms 1931, p. 16). A cut in the finger is an unusual event for the cells
involved and adaptive clotting of blood followed by the growth of tissues
reacting to complex factors result (Arey 1936), but the physiologist would
hardly be inclined to say the reacting cells were intelligent. Such somatic
physiological activity is known to be influenced by hereditary factors as
evidenced by the genetics of haemophilia. The termite behavior recorded
by Hingston seems to me to offer a significant parallel.

Unless the nesting behavior be largely hereditary, there is no more
phylogenetic significance in its evolution than in the evolution of human
architecture. Human architecture seems to rest wholly upon a capacity for
"conditioning" and intelligent response to environmental and esthetic factors.
From the standpoint of behavior analysis, it is in sharp contrast to termite
architecture. Both types of behavior, of course, may be of fundamental
importance to the biological success of the species.

The tendency to resort to anthropomorphic explanations is noteworthy in
observers who are astonished by the remarkable complexity of termite life.
Maeterlinck (1926, 1928) is especially prone to such generalizations. Bugnion
(1927) and Imms (1931, p. 102) resort to the "lapsed intelligence" theory
of Lewes with its Lamarckian implications to explain the origin of "instincts".
All of the references to termite "intelligence" known to the author carry
strong anthropomorphic connotations.

Kemner (1929) has given a classification of the termite nests which he
studied in Java and also discusses the systems of classification used by
Holmgren (1906). In certain respects I find myself in agreement with
Kemner's phylogenetic arrangement—namely in treating the kalotermitid-
type nest as the most primitive and postulating the evolution of the rhino-
termitid-type from the kalotermitid-type. In the arrangement of the
phylogenetic sequence of the various types of termitid nests, however,
I cannot agree with Kemner because the arrangement is opposed to phylo-
genetic sequence based upon a study of the morphological characters of all
the castes (Hare 1937). It would seem to me that all correlated evidences of
phylogeny would have to be considered and certainly comparative morphology
cannot be ignored, not because behavior or physiological characteristics are

less important than morphological characteristics, but the significantly corre-
lated characters which have been studied from a phylogenetic viewpoint are
largely morphological at the present state of our knowledge. Without break-
ing away from the deduced phylogenetic history of the major groups of
termites, one may assume that the most primitive termitids were ground and
log dwellers not differing greatly from the rhinotermitids in their nesting
behavior. Many morphologically specialized termitids have not deviated
much from this basic behavior type. Radiation, however, may conceivably
have occurred in several directions leading to simple ground excavations,
mound nests, fungus-garden construction, arboreal dirt nests, arboreal wood-
carton nests, and other more specialized types, a few of which have been
discussed in the preceding pages. It is not necessary to assume that any of
the more basicly specialized termitid-type nests were derived from any other
specialized type and there is much evidence against this hypothesis. Among
certain closely related groups such as the species of *Apicotermes* and species
of *Cubitermes* and *Procubitermes,* one may postulate evolutionary sequences
which fit the morphological data, but a postulate that *Microcerotermes*-type
nests evolved from *Nasutitermes* (= *Eutermes*)-types and that the fun-
gus-growing behavior was an aftermath of the type of nest-building be-
havior of *Microcerotermes* seems to me wholly out of line with a con-
siderable body of facts upon which the phylogenetic arrangement of these
groups is based.

The separation of analogous from homologous morphological structures
through the maze of genetic modifications, physiological influences, growth
patterns, degenerative changes, and convergent adaptations, is a difficult task.
With increasing knowledge of connecting links and a better understanding of
the principles of embryology and of evolution, we are enabled to rectify many
of the mistaken conclusions of the past. However, in spite of the fact that
the principle of homology has been applied to the evolution of termite nests,
I think that the best available evidence is a parallel series of homologous
morphological structures. Whether homology is assumed for structure, for
behavior or for physiological action, it would seem to rest upon a similar
genetic basis manifesting itself through successions of enzymic effects and
physiological actions and interactions (Wright 1934, p. 33). That behavior
may be dependent at times upon local chromosomal influences has been dem-
onstrated by Whiting (1932) in his studies of the reproductive reactions in
sex mosaics of the parasitic wasp, *Habrobracon.*

I have cited one instance of degenerative evolution of nesting behavior
in the case of *Termes inquilinus.* Degenerative evolution of behavior may
have occurred in numerous instances, but few cases are associated with suf-
ficient data to justify a reasonable conclusion. Degenerative evolution is an
example of a negative and usually non-adaptive directional tendency that
has been a stumbling block for many evolutionary theorists. Modern ge-

netics, however, has shown that mutations are often degenerative in their manifestations, that they may occur at statistically predictable rates, that species characters are usually an outgrowth of gene and chromosome combinations, and that natural selection is probably responsible for keeping wild populations from exhibiting degenerative tendencies of functional characteristics. "Mutation pressure" resulting in degenerative effects might produce a degenerative evolution if selection pressure for a particular structure or function were removed (Wright 1929; Darlington 1936). Degenerative mutations would seem to have more effect in small interbreeding populations. Another positive influence has been postulated (Wright, 1929) in the probable fact that "each character is affected by many genes and each gene affects many characters" (Wright, 1934, p. 30). Thus selection probably does not act upon the single effect, but selects genes and gene combinations which result in a sum total of favorable effects. Consequently a gene or system of genes causing degeneration may be selected for other beneficial effects, particularly if a former beneficial effect has been lost or decreased through a change in the environment.[1] It is thus possible to explain known evolutionary trends on the basis of modern genetic theory without recourse to Lamarckism. Non-adaptive evolution is possible (Wright 1932, p. 363) and it is not necessary to assume adaptive value for every specific character. The multiple effects of genes also give a reasonable explanation of non-utilitarian vestigial structures and recapitulative tendencies. Sudden complete losses of the hereditary basis of complicated structures would probably indicate such gross genetic changes that other vital functions would be affected. It is more probable under natural conditions that the old heredity has merely become overlaid by new heredity suppressing or modifying structures or actions (Wright 1935, p. 105). Needham (1930) emphasizes the opinion that "organs are only recapitulated in so far as they are necessary for the development of the ones which are required in the ontogeny in question, and all the other old ones disappear." Although recapitulative structures and actions may often have functions, it seems difficult to believe all cases are functional and Wright's explanation allows for the possibility of recapitulation of non-functional organs or actions.

I have searched my experience and the literature for a case illustrating vestigial behavior among termites, but I am unable to offer a single instance which is worthy of consideration. In a sphere far removed from the insect world, however, I wonder whether the rather futile action of dogs in scratching dirt following defecation may not be considered an example of behavior which has undergone phylogenetic degeneration, but is still visible as a vestigial pattern (see Enders 1935 for an account of specific differences in faecal behavior of Panamanian cats).

[1] Wright, in commenting upon this statement, adds: "The type allele in each series is that which has the most favorable net effect on all characters. If one character loses in importance relative to others, there will be a shift in the alleles in many series with degeneration of the character losing importance as a consequence of the increased development of the others."

The foregoing discussion emphasizes the phylogeny of inherited species behavior patterns, but I see no reason why individual behavior involving modifiability through experience (Emerson, 1933) may not be characteristic of termites. Such behavior seems to be relatively unimportant in the phylogenesis of the species patterns discussed in this paper. Ranges of variation in the inherited pattern may also be demonstrated under identical environments, and different environments will doubtless bring about variation in the patterns with the same heredity. A better understanding of the ontogenetic development of both genetically and environmentally induced behavior is highly pertinent. These problems await future investigation.

SUMMARY

1. Termite nests may be used as examples of behavior evolution because they are morphological indications of behavior patterns, they express the behavior of a population, the patterns are hereditary, there is a natural control over any Lamarckian influence, evolutionary sequences are available, adaptive modifications may be demonstrated, and coordination mechanisms may be partially analyzed.

2. Wood-eating roaches excavate galleries in wood but make no constructions.

3. The Kalotermitidae excavate wood and construct partitions, indicating responses to humidity and mechanical or chemical factors.

4. The Mastotermitidae exhibit a quantitative advance in nest construction compared to the Kalotermitidae.

5. The Hodotermitidae show a further advance with subterranean nests, elaborate carton construction, and food storage.

6. The Rhinotermitidae have separately evolved subterranean adjustment and in some species show building activities in response to social factors as well as physical factors.

7. Excavated subterranean nests of the Termitidae exhibit the influence of mechanical and spatial factors.

8. Materials used for construction may be dirt, wood, or excrement, cemented by saliva or anal excretions.

9. Structures may include covered tunnels, roads, rain-shedding projections and ridges, nests of characteristic size and differentiation, ventilation pores in the walls, stored food, and fungus gardens.

10. Sterile workers and nymphs of sterile soldiers and workers construct the nests in the Rhinotermitidae and Termitidae.

11. The ecological functions of the nest are control of temperature, control of humidity, and protection from predators and harmful fungi, all enabling the termites to live in otherwise uninhabitable niches.

12. The nesting site may be selected partly or wholly by the colonizing pair, but often is selected by the workers and is followed by a colony migra-

tion. Height of the nest from the ground may be fairly characteristic of the species.

13. Different species within a genus show great divergence in nesting behavior. Species of the genus *Amitermes* have subterranean nests, mound nests, arboreal nests, nests oriented with reference to the sun, and rain-shedding constructions.

14. Convergent evolution of rain-shedding constructions has occurred in the Amitermitinae, Termitinae, and Nasutitermitinae.

15. A discussion of "intelligence," correlation of morphological and behavior homologies, degenerative evolution and "vestigial" behavior is included.

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PHYSICAL ECOLOGY OF THE FIREBRAT, *THERMOBIA DOMESTICA* (PACKARD)

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PHYSICAL ECOLOGY OF THE FIREBRAT, *THERMOBIA DOMESTICA* (PACKARD)

INTRODUCTION

The firebrat, *Thermobia domestica* (Packard), is one of the most common household pests, although not recognized by many people. It is largely nocturnal in its habits, especially if food is plentiful. Being quick and active the insect scurries to shelter behind some object or into some crevice when disturbed or when lights are turned on in a dark room.

Although widespread, this thysanuran has not been studied very intensively, which lack of interest is due largely to the belief among scientists as well as laymen that the life cycle occupies a period of two to three years. The detailed study of the habits and ecology of this pest furnishes much needed information.

SYNONOMY

Thermobia domestica (Pack.)
    Lepisma domestica Pack. 1873
        Packard-5th. Ann. Rpt. Peabody Acad. Sci.: 23-51
    Lepismodes inquilinus Newm. 1863
        Newman-Zoologist f. 1863:8496
    Lepisma furnorum Rovelli 1884
        Rovelli-Zoo. Anz. 8:60
    Termophila furnorum (Rovelli) 1887
        Grassi-Bul. Soc. Ent. Ital. 19:58
    Thermophila furnorum (Rovelli) 1889
        Grassi & Rovelli-Bul. Soc. Ent. Ital. 21
        Oudeman-Tijdschr. v. Ent. 22:425-32
    Thermobia domestica (Pack.) 1890
        Bergroth-Ent. Amer. 6:233
        Packard-Ent. Mon. Mag. 30:155-6

DISTRIBUTION

The firebrat has become very widespread in the tropical and temperate zones. It is likely to be found even in cold regions where heated habitations of man are common. Originally it must have been a warm climate insect. Apparently it received the common name, firebrat, because of its habit of living about outdoor bake ovens in England, where it was well known long before it received its scientific appellation.

FOOD HABITS

It is reported in much of the literature that the firebrat prefers starchy foods of many kinds. Damage to books, records, and other starchy paper materials, especially those having a glazed finish on starchy cloth, and cereal products such as white flour are cited frequently. Very few workers mention

that the insect feeds also on foods rich in protein content, although their cannibalistic habits are mentioned by several. A few observers have emphasized the importance of proteins in the diet of *Thermobia*. Both nymphs and adults feed readily on exuviae, eggs, dead bodies, and even weakened or injured individuals that are unable to resist attack. Investigations of the nutritional requirements of the firebrat are in progress.

METHODS OF HANDLING

The insects were observed and reared in controlled temperature chambers. The relative humidity was regulated by using saturated salt solutions containing an excess of salt, except for the 100% condition, which was obtained by using distilled water. The relative humidity in the containers was determined from time to time with a dew point hygrometer. The salt solutions were placed in pint glass top fruit jars and the insect cages hung in the jars above the solution. These cage bottles were tied to the wire cover clamps on the outside of the jars with a soft piece of string, which pressed into the rubbers when the jars were sealed. The nymph and adult cages were wide-mouthed bottles 50 mm. wide and 70 mm. deep. The mouths of the bottles were 32 mm. wide. The eggs were incubated in vials. The bottoms of the cages were covered with a thin layer of beeswax and sand or other materials to produce a rough surface to enable the insects to gain a better foothold. At first strips of corrugated paper and later strips of paper towels were placed in the cages to serve as hiding and egg deposition places. The strips were long enough to reach across the cages, thus preventing sliding about of the paper. This was important in preventing injury, especially with the early instars.

The food consisted of whole wheat flour or Mead's Cereal, a prepared food of known composition, and dried lean beef. Beef relatively free of fat was desirable and was preferred by the insects. The addition of the shredded meat apparently produced a diet much superior to cereals alone. An excess of food was added at each feeding so that ample was present at all times. The food in the environments in which the humidities were 97 and 100% was placed on paper strips to facilitate removal. Frequently the insects scattered a portion of the food over the bottom of the cage. Small brushes were used to aid in removal of fungous growth and particles of food that adhered to the bottom of the cage. Rubbing a finger around the curved neck of the cage bottles to remove dust particles of food was sufficient to prevent escape of the insects.

The sealed jars were opened and the insects examined as frequently as necessary depending upon the environments and the information desired. The insects in environments in which humidities were 97 and 100% were examined and the food changed daily because of the excess moisture that accumulated in the food and the growth of fungi in temperatures below 37°

C. The insects could tolerate being sealed in the jars for extended periods. The longest period was 3 months during the summer at room temperature, when some of the cages contained as many as half a dozen specimens. No apparent injury was produced by the gaseous environment in any of the cages except with certain salt solutions which decomposed. Where this occurred, decomposition took place immediately on starting the test and not after extended periods.

It greatly facilitated determination of the sexes in the early instars before the ovipositor became visible from a dorsal view, to observe microscopically the reflection of the ventral surface of the abdomen in a mirror. The nymphs were placed in shell vials about one-half inch in diameter and cut to about the same height, and this container placed on the mirror held at an angle so that the reflection of the specimen could be seen.

EGG STAGE

Description. The eggs of *Thermobia* are soft, white, and opaque when laid although the chorion is transparent. The chorion soon hardens, becomes tinged slightly with yellow, and the opacity of the egg usually increases. The eggs typically are elliptical in shape, but may be slightly bean-shaped or roundly pointed at one end. They are about 1 mm. long and 0.7 mm. wide in the greatest dimensions. The chorion of the freshly laid egg is smooth and devoid of sculpturing. However, Adams (1933a, b) states that the chorion is shiny and smooth with sparce minute markings. On about the third day at 35° C. distinct markings appear on the chorion, apparently produced by the cells of the embryonic tissues that are in intimate contact with it. The embryo is visible through the chorion on about the fourth day. The portion of the egg not occupied by the body of the embryo appears to be filled with a rather clear fluid. The pigmented eyes are evident by the eighth day. By the ninth day the legs are visible and movement of the embryo when the egg is disturbed is discernible. The liquid contents appear to be absorbed on about the thirteenth, and hatching occurs on about the fourteenth day. Some wrinkling of the chorion may occur during the early stages of development, but in favorable environments is rounded out again toward the end of embryonic development.

Hatching. Emergence is effected with the aid of an egg burster on the anterior portion of the head and by pressure which breaks the chorion. In unfavorable environments, especially the dry ones, the nymphs may be unable to break the chorion or may die when only partially emerged. This may occur when only an antenna or as much as the head and thorax are external. Frequently the abdomen is not extricated until the first molt (Sweetman, 1934). This is true especially in dry environments.

Response to Temperature and Moisture. Eggs were exposed in temperature and moisture environments ranging from 20° to 50° C. and relative

TABLE 1. THE INCUBATION PERIODS OF *Thermobia* EGGS EXPOSED AT VARIOUS
TEMPERATURES AND IN VARIOUS HUMIDITIES.

Temp. °C.	Relative humidity	Number of eggs	Number hatched	Percentage hatched	INCUBATION PERIOD	
					Range in days	Average number of days
20	77	32	0	..	.....	..
22	100	3	0	..	.....	..
22	77	38	0	..	.....	..
22	51	3	0	..	.....	..
22	32	5	0	..	.....	..
22	14	3	0	..	.....	..
24	77	14	3	21	74–80	77
27	100	16	11	69	42–45	44
27	97	8	7	88	41–47	44
27	77	13	12	92	42–48	46
27	56	17	14	82	41–49	45
27	32	9	7	78	46–51	48
27	12	14	7	50	44–50	46
29	100	25	16	64	31–35	33
29	97	22	20	91	29–36	33
29	85	20	18	90	31–37	32
29	77	21	19	90	31–34	32
29	62	21	18	86	31–38	33
29	56	21	20	95	30–34	32
29	32	25	21	84	29–32	31
32	100	24	19	79	18–23	22
32	96	23	20	87	21–23	22
32	77	29	26	90	18–22	20
32	64	9	8	89	21–24	22
32	52	13	11	85	19–22	21
32	32	24	19	79	19–23	22
32	12	20	19	100	18–24	21
37	100	25	23	92	11–15	13
37	96	16	14	88	11–13	13
37	85	8	8	100	14–15	14
37	76	157	146	92	10–14	12
37	51	19	14	74	11–15	13
37	48	13	12	92	11–14	14
37	32	20	19	95	11–13	12
37	12	15	13	87	10–14	12
40	100	14	9	64	10	10
40	96	27	23	85	9–10	10
40	85	13	12	92	9–13	11
40	83	12	21	100	9–10	10
40	76	8	5	63	11–12	11
40	54	36	31	86	9–11	10
40	12	5	4	80	10	10
41	96	6	6	100	9–11	10
41	76	5	4	80	9	9
41	54	9	6	67	8–10	10
41	32	10	9	90	10–11	10
42	100	16	6	38	9–10	10
42	96	36	26	72	8–11	9
42	85	16	13	81	8–12	10
42	76	19	17	95	7–10	9
42	50	17	15	88	9–10	10
42	32	6	3	50	10	10
42	12	4	2	50	9–10	10
44	100	5	5	100	7	7
44	96	10	8	80	7– 9	8
44	86	9	5	56	7–11	8
44	82	5	2	40	9	9
44	79	8	3	38	9–11	10
44	76	29	22	76	7– 9	9
44	50	11	11	100	7–10	9
44	32	14	10	79	9–10	10
44	12	5	4	80	9–10	9
47	100	11	2	18	11–12	11
47	83	9	9	100	9	9
47	76	56	39	70	8–15	11
47	50	18	17	94	9–10	9
47	32	1	1	100	9	9
47	12	9	0	0	.....	..
48	75	25	0	0	.....	..
49	75	24	0	0	.....	..
50	75	83	0	0	.....	..

humidity of 12 to 100%. The eggs failed to hatch at 20° and 22° C., although some development occurred (Table 1). A large majority of the embryos developed to maturity at 24° C., but only 21% of the total number of eggs hatched. The nymphs from these eggs were very weak and died in a few days without molting. Further evidence of the injuriousness of this low temperature to the developing embryos is shown by eggs that were transferred to 37° C. after 41 days exposure at 24° C. Five eggs were transferred, three embryos developed, but only two hatched after 7 to 8 days exposure at the higher temperature. One nymph was apparently normal and lived. Nymphs emerged from eggs exposed at 27°C. in 41 to 51 days. Above 27°C. a rapid reduction in developmental time occurred for each degree rise in temperature to 37° C., being 33 days less at this latter temperature than at 27° C. and over two months less than at 24° C. Adams (1933a) reported that 15 days was usually necessary for incubation of the eggs at 37° C. However, when the temperature was carefully measured in the immediate vicinity of the eggs, the average time was twelve to 14 days. About 14 to 15 days are necessary for embryonic development at 35°C. Above 37°C. the decrease in the length of the incubation period with a rise in temperature continued until the shortest period was reached at 44° C., where 7 to 11 days was sufficient. Exposures at 47°C. resulted in a lengthening of the incubation period to 8 to 15 days (Tables 1, 2). None of the eggs hatched above 47°, although some development occurred at 48° C. Short exposures at 48° C. were not always fatal. Eggs exposed at 48° C. for one week, then transferred to 37° C. hatched after 7 to 10 days exposure at the lower temperature. One embryo, well developed at a favorable temperature, hatched about a day after being exposed at 49° C.

No consistent effects of moisture are evident at the different temperatures in so far as shown by the length of the incubation period. When the per-

TABLE 2. THE AVERAGE DEVELOPMENTAL PERIOD AND THE AVERAGE PERCENTAGE OF HATCH OF *Thermobia* EGGS EXPOSED AT VARIOUS TEMPERATURES AND IN VARIOUS HUMIDITIES.

Temp. °C.	Average incubation period. Days	Average hatch. %	(x — n)y values
20	....	0	.....
22	....	0	.....
24	77.2	21.4	.....
27	45.3	75.3	135.9
29	32.3	85.1	161.5
32	21.3	86.6	170.4
37	12.4	90.5	161.2
40	10.2	83.5	163.2
41	9.8	83.0	166.6
42	9.5	72.8	171.0
44	8.9	74.0	178.0
47	11.0	69.8	253.0
48	...	0	.....
49	....	0	.....
50	....	0	.....

centage of nymphs hatching is considered, the effects of moisture are very noticeable (Table 1). At 27° and 29° C. a large percentage of the nymphs hatched in relative humidities of 32 to 97%, while most of the eggs hatched at 32° and 37° C. in all humidities. A humidity of 97 to 100% favors development of fungous attack, especially at 27°, 29°, and 32° C. The developing embryos were destroyed frequently by fungi a few days before hatching. The fungi were not so troublesome in temperatures of 37° C. or above. The percentage of embryos maturing in the various humidities was somewhat variable in temperatures of 40° C. and above, indicating an inhibiting effect, but was high in most humidities. Only 50% of the eggs hatched in 12% humidity at 27° and none at 47°C., although good hatches occurred in 12% between these temperatures.

It appears that the chorion of *Thermobia* eggs is sufficiently impervious to loss of water in most humidity conditions during the short incubation periods at high temperatures to prevent a lethal effect from loss of water. When the incubation period was much prolonged as occurred at 27° C., the eggs became much wrinkled in 12% humidity and a number of the nymphs had difficulty or failed to emerge from the egg. At times the fully matured embryos could be observed moving in the egg several days after the normal period for hatching had passed, and were apparently unable to break the chorion.

Another evidence showing the effects of the environmental conditions on incubation is the relative size and vigor of newly hatched nymphs. Those hatching at 37°C. and 76 to 85% humidity were plump and vigorous. Specimens hatched in 12 and 32% humidity at 32°, 29°, and 27° C., especially in the latter, were small and weak, but frequently recovered if exposed in favorable environments. None of the nymphs completed the first instar that hatched at 24° C. The same was true of many of the nymphs hatched in all humidities, but especially the dry environments at 42°, 44°, and 47° C. Many of the embryos died after becoming well developed in all humidities at 27° and 42° to 47° C., and in 100% humidity at 29° and 32° C. A number of the nymphs died in all humidities during the process of hatching at 42°, 44°, and 47° C. Many nymphs had the abdomen remaining in the egg chorion in all humidities at 27° and 42°C. and above, and the 12% and 32% humidities at 32°, 37°, and 40° C. Frequently the nymphs did not free themselves from the egg chorion until the first molt.

Apparently the optimum temperature and moisture environment for incubation of the eggs is near 37°C. and 76% to 85% relative humidity. Reference to Table 2 brings this out more clearly regarding temperature. The incubation period was shortest at 44°, but the highest percentage of eggs hatching was at 37°C. The nymphs hatched at 37°C. with favorable moisture conditions were strong and plump, while many were weak at the higher temperatures.

Threshold of Development. The threshold of development was further

determined by plotting the reciprocal of the time-temperature curve (Fig. 1).
This curve crosses the base line at 24°C. This indicates that the lowest
temperature at which a high percentage of normal nymphs could be expected
to hatch would be near 25°C. This is in agreement with experimental data
(Tables 2, 3). Apparently the straight line portion of the curve extends
from about 28° to 40°C. An examination of the (x-n)y values (Table 2)
indicates that 27° and 42° to 47°C. are beyond the straight line portion of
the curve. The average daily development at 32°C. appears to be nearer
4.9% than 4.7% as found.

Eggs can be exposed at temperatures below the threshold of development
for as much as 6 weeks and still hatch, if placed later in favorable environ-
ments (Table 3). The nymphs from such eggs apparently are normal. The
effects of moisture are not evident at such low temperature conditions, as
eggs hatched that had been exposed in relative humidities ranging from 12
to 100%. The data from several lots of eggs are combined in the table.
Since some of the eggs in all lots hatched, it appears that all or most of
the embryos, if under favorable conditions, were capable of normal develop-
ment. Nymphs hatched from about one-third of these eggs following ex-
posures in favorable environments. Fourteen of the eggs were held at or
below the threshold temperature for 49 days and still five of them hatched.
Longer exposures at low temperatures killed all the embryos. Apparently a
slight amount of development occurred at low temperatures as a number of
the embryos showed a shorter incubation period after exposure at 37° than
with continuous exposure at 37°C. A very evident embryonic development
occurs at 24°C. although few eggs hatched (Table 2).
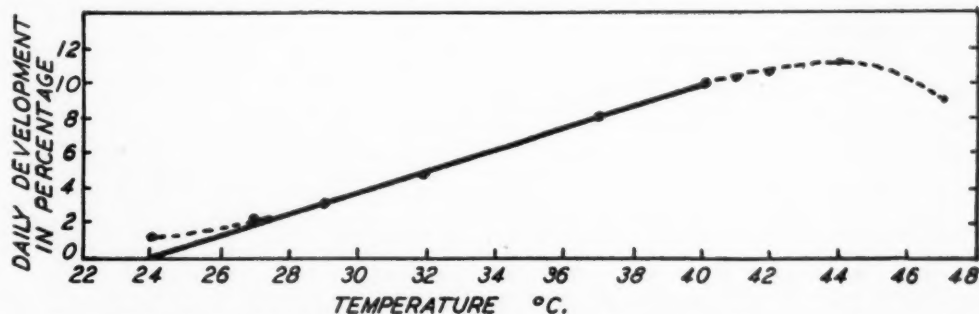
FIG. 1. The threshold of development for eggs of *Thermobia* when exposed at various
temperatures and in various humidities.

NYMPHAL STAGE

Description. The newly hatched nymphs are about 2 mm. long, omitting
the appendages. They are white, opaque, and free from scales or the ventral
abdominal styli. The first instar is more plump and sluggish than later in-
stars. The tip of the abdomen following the first molt is more pointed, the
antennae and caudal filaments are greatly increased in length, and the body
wall is shiny and tinged with yellow in contrast with the milky white and

opaque appearance of the newly hatched nymphs. The ventral abdominal styli are absent. The body length following the first molt is only slightly increased.

TABLE 3. THE EFFECTS OF LOW TEMPERATURE ON EMBRYONIC
DEVELOPMENT OF *Thermobia*.

Number of days at low temperature. °C.	Number of days at high Temperature. °C.	Number of eggs	Number hatched
19° to 22°	*32°*		
34	. .	2	0
84	. .	1	0
19° to 22°	*37°*		
8–10	15	3	2
13–16	8–12	13	5
17–20	10–14	8	3
21–24	12–14	10	3
28–31	13–15	4	2
34	. .	4	0
39–42	15	5	1
19° to 21°	*37°*		
44–47	7–9	9	4
49–51	9	14	5
58	. .	1	0
66	. .	1	0
73	. .	1	0
84	. .	1	0
22° to 26°	*32°*		
60+	. .	39	1
60	8	5	2
22° to 26°	*37°*		
41	8	5	2
60	8	15	4

Early Instars. The nymphs are clothed with scales in the fourth and following instars, except when the scales are rubbed off (Sweetman, 1934). Preceding the third ecdysis for a few hours the scales on the new cuticle can be seen through the old cuticle. This was observed by Adams (1933b) also. The number of days spent in the early instars at 37°C. by 6 nymphs is given in Table 4. One day or less is spent in the first instar, about 4 in the second, about 6 in the third and fourth, approximately 8 days in the fifth to the eleventh, with the period gradually increasing to about 12 to 13 days in later instars. The number of instars depends entirely on the length of the life of the individual. Many pass through from 45 to 60 instars before death. This phenomenon is being reported in more detail in a separate paper (Sweetman & Whittemore, 1937). ·

The first pair of ventral abdominal styli appears at the fourth molt (fifth instar). The second pair of ventral abdominal styli usually appears on attaining the seventh or eighth instar. The males (see adults) do not ordinarily acquire the third pair of ventral abdominal styli as do the females, which usually acquire this pair in the tenth instar. The number of segments

of the antennal and caudal appendages increased rapidly during the first few instars, but no accurate count was made.

No distinctive sex characters were observed on living specimens before the eighth instar, at which time the posterior abdominal sternites begin showing the notched appearance which lengthens into a definite slit by the time the ovipositor appears. About 10 instars are passed at 37°C. before the ovipositor is visible from a dorsal view.

TABLE 4. THE EARLY INSTARS OF NYMPHS OF *Thermobia* AT 37°C. AND IN RELATIVE HUMIDITY OF 75 AND 84%.

Sex	INSTARS—Days in Each									
	1	2	3	4	5	6	7	8	9	10
♂	1	4	6	6	6	7	7	8	8	9
♂	1	4	7	8	12	7	6	6	9	10
♀	1	4	6	6	7	10	9	10	11	..
♀	1	4	6	6	6	7	6	8	6	9
♀	1	4	6	6	8	7	7	7	7	7
♀	1	4	6	6	8	7	8	..	(16)	10

It greatly facilitated the ease of determining the time of molting to amputate one or more of the antennae, cerci, or the caudal filament. Appendages were regenerated after repeated amputations of the same appendage throughout the life of the insects (Sweetman, 1934). Occasionally more than one molt was necessary before normal appendages developed. This frequently was manifested by the beaded appearance of the terminal segments of an appendage during the interval of regeneration.

The young nymphs have a habit of feigning death in the early instars. This habit is discontinued gradually and is seldom exhibited after nymphs become about one-third grown. The color pattern is approximately the same in nymphs and adults, although more definite in the latter. The pigment is in the scales and the pattern is destroyed if the scales are removed. In moist environments, however, the scales may become more deeply pigmented and the light and dark areas of the pattern tend to blend together.

Responses to Temperature and Moisture. Newly hatched nymphs were exposed to a wide range of experimental conditions. The environments varied from 22° to 47°C. and 12 to 100% relative humidity (Fig. 2, Table 5).

None of the nymphs matured in environments below 27° and only a few at 27°C. The greatest length of life at 22°C. was 47 days, showing that this temperature is much too low for normal development. The length of life at 27°C. was much greater. Twelve nymphs lived from 100 to 200 days and 11 from 201 to 294 days, but apparently none of these were mature when death occurred. Five nymphs, 7% of the total, reached maturity at 27°C. Forty-three per cent of the nymphs matured at 32°C. Sixty-six per cent of the nymphs matured at 37°C., but higher temperatures were less favorable. A sharp reduction in the percentage maturing resulted at tem-
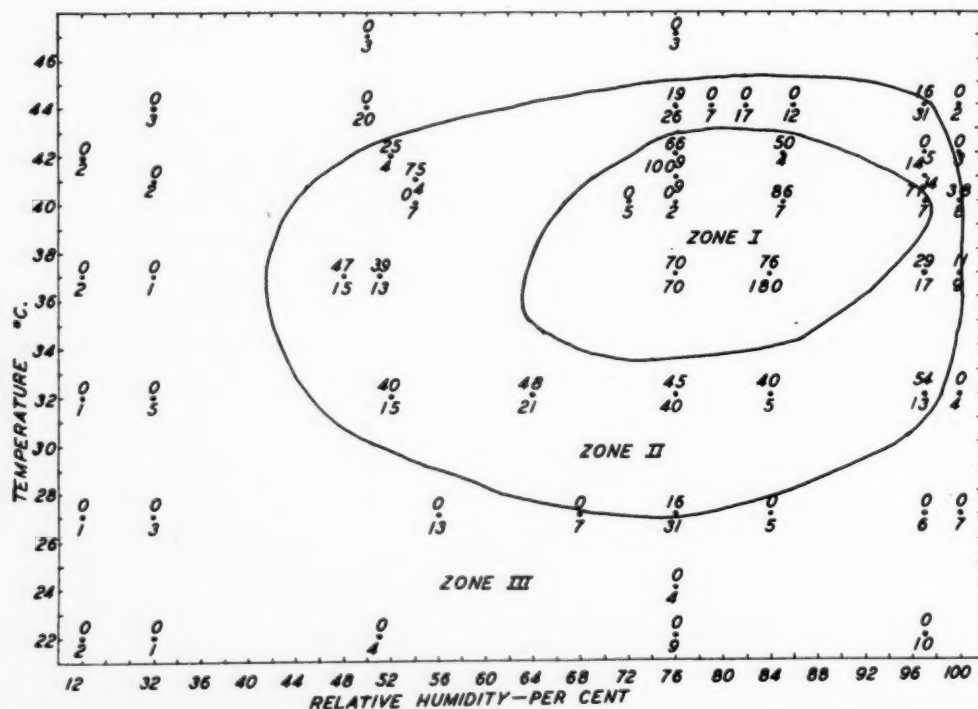
FIG. 2. The percentage of nymphs of *Thermobia* that matured at various temperatures and in various humidities. Figures above dots indicate percentage that matured; those below dots, number of nymphs exposed.

peratures between 42° and 44°C., only 9% completing development at the latter. All of the nymphs died in a few days at 47°C., mostly during the first few days after exposure. The first few instars seem to constitute a very critical period for the nymphs and many hatch that apparently are not capable of maturation even in favorable environments.

Fifteen nymphs (not shown in Fig. 2, Table 5) were exposed to approximate temperatures of 41°C. for about 3 weeks, followed by 44°C. until

TABLE 5. THE PERCENTAGE OF NYMPHS OF *Thermobia* WHICH MATURED AT VARIOUS
TEMPERATURES AND IN VARIOUS HUMIDITIES.

Temp. °C.	PERCENTAGE MATURED IN A HUMIDITY OF						Total. %
	12-32 %	48-56 %	64-68 %	72-79 %	82-86 %	97-100 %	
22............	0	0	..	0	..	0	0
27............	0	0	0	16	0	0	7
32............	0	40	48	45	40	41	43
37............	0	43	..	70	76	23	66
40............	0	0	..	0	86	53	40
41............	0	75	..	100	..	14	48
42............	0	25	..	66	50	0	33
44............	0	0	..	15	0	15	9
47............	0	0	..	0	..	..	0
Total %.......	0	22	36	44	64	21	

death or maturation took place. The relative humidities were 54%, 76%, and 96%. Maturation occurred in each environment; 53% of the nymphs matured. This is a much higher percentage of maturation than occurred when nymphs were exposed continuously at 44°C. This indicates that the young nymphs can tolerate 41° much more readily than 44°C.

None of the nymphs matured in relative humidities of 12% and 32% at any temperature (Fig. 2, Table 5). Newly hatched nymphs may withstand these humidities for a few days. None were exposed between 32% and 48% to 53%, but maturation occurred in the latter environments at temperatures ranging from 32° to 42°C. A large percentage of the nymphs can be reared to maturity in 76% to 85% relative humidity at 37° to 42°, but the number maturing decreases decidedly at 44°C. Relative humidities of 97% to 100% are decidedly unfavorable, the majority of the nymphs failing to reach maturity. Part of this unfavorableness was produced by the dampness of the food and sides of the cages which resulted in the nymphs drowning or adhering to the food. Also, fungi in which the nymphs become entangled attack the food more readily in the high humidities, especially below 37°C. The higher humidities were more favorable than low humidities when the temperatures approached the upper limits of tolerance. No definite effects of moisture, in environments where maturation was completed, on the time required for development was detected.

Zones of temperature and moisture combinations that have approximately equal effects on development are evident. Zone I (Fig. 2) demarks approximately the optimum environments for development, where a large percentage of the nymphs can be reared in a relatively short time. The responses to optimum temperature in favorable moisture conditions is shown more plainly in Table 5. Zone II roughly demarks conditions where 50% or less can be reared to maturity. Zone III shows environments that are so unfavorable that none of the nymphs can be reared to maturity.

The length of the period of development from hatching to maturation definitely shows the response to temperature very strikingly (Table 6). No definite criterion denoting maturation could be detected (Sweetman, 1934). Adams (1933a,b) states that sexual maturity is attained in about 11 to 12 weeks at 37°C. after numerous molts. This study indicates that the usual period from egg to egg is greater, although individuals only 7 to 8 weeks old have reproduced. The criterion used to designate maturation in this study is an arbitrary one and is based on the females only. When the ovipositor became visible from a dorsal view, the animals were considered mature. This, at least, serves to show the relative values for the various environments. An extremely wide variation in the number of days necessary for maturation of the nymphs occurred in most environments. This was true frequently among nymphs from the same lot of eggs and reared in the same cage, where the physical environment and food were uniform.

TABLE 6. The length of the period of development of *Thermobia* nymphs from
hatching to maturation and reproduction. The figures followed by *a*
include a number of which the sex was not determined.

Temp. °C.	Number Matured		Days to Mature Females		Age at First Oviposition	
	♂	♀	Range	Average	Range	Average
22	0	0	......	...	...	...
27	2	3	308–430	330	...	...
29	10	10	207–371	247	...	...
32	35a	10	65–197	105	138	138
37	46a	27	32–165	92	60–142	113
40	7a	7	63–124	93	109–191	150
41	8	6	28–60	47	47–64	56
41–44	4	4	33–65	42	...	...
42	7a	2	108–125	117	...	...
44	7a	3	38–41	40	...	...

A very rapid reduction in the days necessary for maturation occurred in en-
vironments from 27° to 41°C. The period before reproduction occurred was
not so definite, probably because of the small number of females involved,
and also because the requirements for fertilization (see adults) were not so
well understood when this test was made.

A check of the sources of all nymphs in relation to the possible influence
of parentage and environment showed that some individuals matured from
eggs from every parent which deposited eggs. Of course this occurred
only when the eggs were placed in favorable environments. Nymphs ex-
posed at 22° and 27°C. had hatched at higher temperatures and some detri-
mental effect may have resulted by change to the lower temperature.

Effects of Low Temperature. Several groups of nymphs from one-fifth
to fully developed were collected in the laboratory and exposed suddenly
to low temperatures at various times during the winter. A summary of the
observations follows:

Active .... 8° and above
Sluggish .... 0° to 7°
Inactive .... 0° and below
Survived .... 0° to -15.5°
Died .... 0° to -17°

The results must be considered approximate as the time of exposure and
variation in temperature was great. It appears that continued exposures of
0°C. or slightly lower are sufficient to kill the nymphs in 4 weeks or less,
although several survived much lower temperatures for a few hours. Speci-
mens exposed to cold frequently showed injuries from the exposures, being
partially paralyzed. Recovery, if any, was slow and injury was evident for a
week or more.

Solitary and Group Rearing. A number of nymphs were exposed at 32°
and 37°C. in a relative humidity of 76% to determine the possible effects
of group or solitary confinement. Records of the number living were made

at intervals of about 10 days, when the cages were cleaned and new food added. This assisted in keeping the temperature and moisture environments almost constant throughout the tests. Solitary confinement in these environments appeared to be very unfavorable to maturation. The largest percentage was reared at both temperatures when a number of nymphs were placed in 1 cage. Twenty-seven nymphs matured in 1 cage. The data show that crowding can be rather extreme and still large numbers will mature. However, heavy mortality of newly hatched nymphs frequently occurs in 76% humidity, although it is a suitable condition after the nymphs are 1 month old. This experiment was repeated at 37°C. and in a relative humidity of 84% (Table 7). The jars were opened and cleaning of the cages and addition of new food took place at three-day intervals, because of the development of fungous growth if left undisturbed longer. Detailed records of the nymphs were kept for a period of 3 months. Eighty-five per cent were large enough at that time for the sex to be determined while alive. It is evident that this humidity at 37°C. is far superior for percentages maturing to 76% relative humidity. This suggests that crowding produced an environ-

TABLE 7. THE EFFECTS OF CROWDING ON DEVELOPMENT OF NYMPHS OF *Thermobia* AT 37°C. AND IN 84% RELATIVE HUMIDITY.

Number at start	Number matured	Percentage matured	Age of nymphs that died. Months	Relative sizes
1	1		..	Large
1	0		2.5	..
1	0	60	2	..
1	1		..	Large
1	1		..	Small
5	5		..	Large
5	4	93	0.5	1 Small
5	5		..	2 Small
11	8		.25–2	4 Small
10	4	52	.5–1	2 Small
10	5		.25–2	Small
11	5		.25–2	3 Small
15	13		1.5–2	Small
15	14	73	1.5	12 Small
15	6		.5–1	3 Small
23	12		.25–1	6 Small
21	19	76	.5–1	16 Small
22	18		.25–2	15 Small
20	16		.25–2.5	12 Small

ment slightly more favorable in a humidity of 76%. This seemed especially true with the very young stages. However, development (size) was somewhat greater among isolated individuals and small groups than among large groups as indicated in the last column in Table 7. This suggests that about 5 individuals per cage was best, as a high percentage of large individuals was produced in 3 months. In large stock cages where ample space was available

there was a strong tendency for all stages to collect in groups where the temperature and moisture conditions were favorable. This was also true of adults (see next section).

ADULT STAGE

Size. Growth continues long after the arbitrary criterion for maturation used in this work, and long after the first eggs are laid. Females frequently more than doubled in both length and weight after their first oviposition. Large specimens attain a weight of about 40 mg. and a body length of 14 mm. (40 mm., if appendages are included). The rate of growth decreases with older specimens, apparently becoming very slight or stationary with many mature specimens.

Mating. The mating process of the firebrat is different from that of higher insects. Spencer (1930) apparently observed mating, but described it merely as a "love dance". The males are most active during the procedure, which starts with the male and female facing each other. The male approaches the female and repeatedly contacts her antennae with his; then he approaches closer and contacts or senses the head of the female with his mouthparts. The female lowers her head and raises her thorax slightly. Her antennae respond slightly to those of the male. The male may rest for a few seconds or minutes after contacting the antennae or head of the female or may turn and crawl away for one-half to two-thirds of an inch and repeat the movements. The male moves the head fairly rapidly from side to side while going toward or away from the female. Soon the male, while moving toward or away from the female, will curl the tip of the abdomen to one side and upward as far as possible with a quivering motion and turning from one-half to completely around with the abdomen in the air. The head is turned slightly in the same direction as the abdomen while whirling. The whirling is always in the direction in which the abdomen is curled, but the adbomen may be curled to the right or left at different times. The curling of the abdomen and whirling may be repeated several times in succession or may be interspersed with only crawling and contacting the female as described at the beginning. At frequent intervals, the male after contacting the head of the female, turns aside and passes the female contacting her legs as he passes. The female then moves forward for about three-fourths of an inch, slowly moving the head from side to side, then turns directly around and faces the male. The male repeats the actions described above. Following a series of curling and whirling movements, the male while twisting the abdomen from side to side and quivering the antennae, deposits the spermatheca on the surface about one-half inch in front of the female. Then the male goes, somewhat more rapidly than previously, to the female and contacts her head and passes by contacting her legs as previously described to a point about 1 inch beyond the female and comes to rest. He shows no

further interest in the female and in 5 to 10 minutes moves away. The male devotes attention to the female for 20 to 35 minutes before depositing the spermatheca. The female immediately on being touched by the male moves forward as mentioned before, straddles the spermatheca and passes on until certain reproductive structures contact the spermatheca. In less than a minute the female has attached the spermatheca, and then turns around and contacts or tastes the spermatheca with her mouthparts. Within 2 to 3 minutes the female begins biting off and eating bits of the spermatheca at intervals of about 1 minute. Twelve to 50 minutes after attaching the spermatheca, the female consumes the remaining portion of it, and thoroughly cleanses the reproductive structures.

Oviposition. Eggs are deposited in crevices, food, or other available places. A female ready to oviposit moves the tip of the ovipositor from side to side searching for a crevice or soft material while slowly crawling about. Apparently females depend upon contacting their ovipositors with a suitable surface rather than on other senses. Once a suitable place is located the ovipositor is inserted as far as possible before eggs are laid. Apparently the females prefer crevices where the eggs can be hidden. In cages, where no other material was available, the eggs were deposited in the food, or scattered loosely on the bottoms of the cages. Frequently the eggs were flattened or otherwise pressed out of shape by the walls of the cavity surrounding them. Adams (1933a) reported 'similar observations. This distortion must be quite extreme to fatally injure the developing embryo. Occasionally the resulting nymph from such eggs will be misshaped by having a concavity in the head capsule or other part of the body, which disappears on hatching or after molting.

Oviposition Response to Temperature and Moisture. Adults were exposed for long periods of time in various temperature and moisture conditions to determine the influence of these physical factors on reproduction. The environments varied from 22° to 52°C. and the relative humidity from 12% to 100%.

The oviposition records of 215 females which were exposed in the various environments are shown in Figure 3. Results show definite limitations of temperature and moisture in so far as oviposition is concerned. Eggs were developed and laid at 4 different temperatures, 32°, 37°, 40°, and 41°C. Captured females, however, at times oviposited a few days after exposure to temperatures that were unfavorable for development of eggs. This occurred at temperatures ranging from 22° to 42°C. inclusive. No oviposition whatever took place in temperatures above 42°C. A few mature females were exposed at 22° and 27°C. continuously until death. They lived for long periods of time, but no reproduction occurred. A number of males and females were reared and maintained at 27°, 29°, and 32°C. None reproduced at 27° and 29°C. and only a few at 32°C.
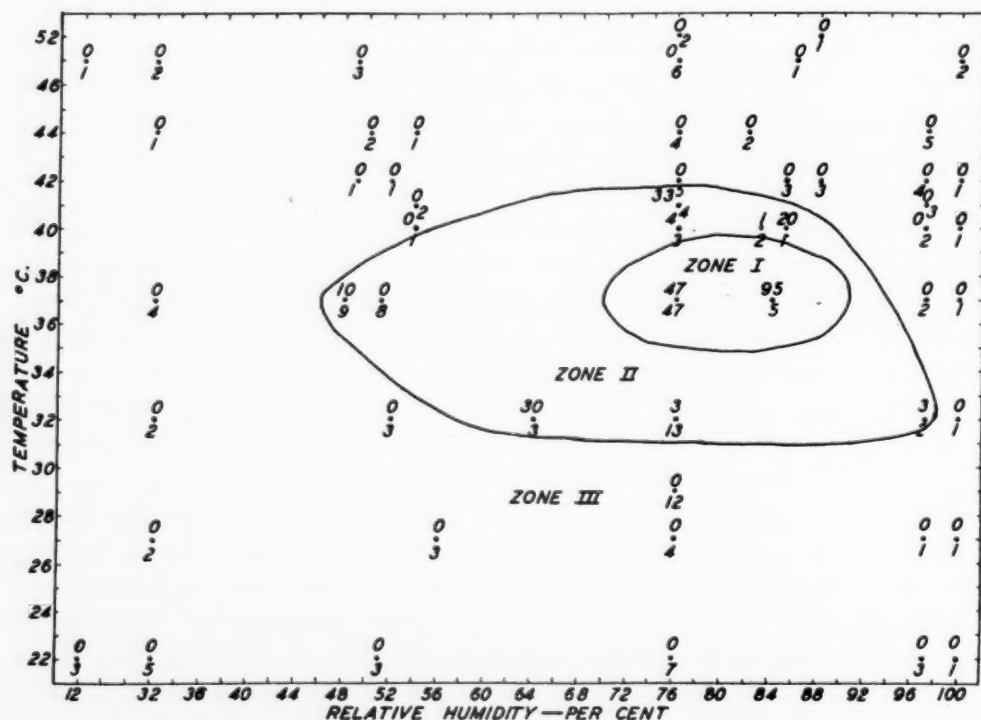
Fig. 3. The oviposition response of *Thermobia* when exposed at various temperatures and in various humidities. Figures above dots indicate average number of eggs per female; those below dots the number of females.

Deposition of eggs occurred in relative humidities ranging from 48% to 97%. A humidity of 84% with favorable temperatures was superior to that of any tested and appears to be near the optimum for egg production (Fig. 3, Table 8). The only moisture condition in which females were exposed at all temperatures used in the tests was 76% (Table 8). Stock cages containing a number of individuals in 76% humidity at 37°C. have consistently yielded large numbers of eggs. When additional males were added to cages that contained non-ovipositing females in favorable environments, oviposition then frequently took place in from 2 to 4 weeks (see fertilization).

Three zones (I, II, & III) showing oviposition response to temperature and moisture can be roughly demarked. Zone I shows the approximate limits of the most favorable region for reproduction. Apparently the optimum temperature and moisture environment for reproduction is near 37°C. and 84% relative humidity. Zone II demarks a region where reproduction occurs and the species could maintain itself, although it would not likely become abundant in such environments. None or very little reproduction will occur in Zone III, and the firebrat could not maintain itself if exposed in such environments continuously.

A few females had reached the maturation stage when 1 month old in

environments at 37° to 41°C. These females began ovipositing when 7 to 8 weeks old. Three females that matured at 27°C. reached maturation when 308, 353, and 430 days old. All were reared in the same cage. This temperature is very near the minimum at which maturation occurs. Incuba-

TABLE 8. THE OVIPOSITION RECORDS OF *Thermobia* EXPOSED AT VARIOUS TEMPERATURES IN A CONSTANT RELATIVE HUMIDITY OF 76%.

Temp. °C.	Numer of ♀♀	NUMBER OF EGGS		
		Lots	Number	Average per ♀
22	7	0	0	0
27	4	0	0	0
29	12	0	0	0
32	13	3	44	6
37	22	57	1094	50
37	25	..	1118	45
40	3	1	12	4
41	4	6	130	33
42	5	0	0	0
44	4	0	0	0
47	6	0	0	0
52	2	0	0	0

tion (Table 1) and development to the adult stage (Table 6) take place in about 1 year at this temperature. Reproduction, however, does not occur. It has been assumed generally that the life cycle of *Thermobia domestica* requires 2 to 3 years for completion of development. Apparently there is no basis for this general assumption.

Detailed records of reared females that were kept in favorable conditions and continuously with males show that oviposition may occur when females are 1.5 to 4.5 months old at 32° to 41°C. (Table 6). The youngest female to deposit eggs was reared at 41°C. and 76% humidity. Oviposition took place when this individual was 47 days old.

The individual oviposition records of a number of females that laid eggs are shown in Table 9. The stock either was collected or reared from eggs. The captured females were mature or nearly so when first exposed to the experimental conditions and perhaps had laid a number of eggs preceding capture. There was much variability among the different females that reproduced, both as to the number of lots of eggs and the total number of eggs laid. The variation was from 1 to 195 eggs, with an average of about 50 eggs per female. The greatest number of eggs laid was by a reared individual. During 3 summer months this female was kept at room temperature. A total of 195 eggs in 6 lots was oviposited during its life of 404 days. The first lot containing 32 eggs was laid when the female was 77 days old and the last lot of 35 eggs when 358 days old. One lot, the fourth, contained 45 eggs.

A series of females was tested to determine if a greater number of eggs was laid if exposed singly or in groups (Table 10). A wide variation occurred

TABLE 9. THE NUMBER OF EGGS LAID BY OVIPOSITING FEMALES OF *Thermobia* AT
VARIOUS TEMPERATURES AND IN VARIOUS HUMIDITIES.

Temp. °C.	Relative humidity	Number ♀	Number of Eggs		Reared or captured
			Lots	Totals	
32	64	1	6	90	R
32	76	1	2	32	C
32	76	1	1	12	R
32	76	1	1	3	C
32	97	1	1	6	C
37	48	1	4	52	R
37	48	1	4	42	C
37	51	1	1	1	C
37	76	1	1	11	R
37	76	1	6	195	R
37	76	1	3	28	R
37	76	1	1	32	C
37	76	1	1	32	C
37	76	1	3	61	C
37	76	1	3	63	C
37	76	1	3	41	C
37	76	1	2	21	C
37	76	1	6	183	C
37	76	1	7	81	R
37	76	1	1	13	R
37	76	1	5	75	R
37	76	1	2	25	R
37	76	1	1	31	R
37	76	1	2	33	R
37	76	1	12	169	R
37	76	5	..	127	R
37	76	5	..	277	R
37	76	5	..	191	R
37	76	5	..	287	R
37	76	5	..	236	R
37	84	3	..	365	R
37	84	1	11	108	R
40	76	1	1	12	C
40	83	1	1	3	C
40	85	1	1	20	R
41	76	1	3	67	R

among both individual and group cages, although the average was greater among the group cages. However, the average number of eggs per female is quite similar to that shown in Table 9. Since females can be fertilized only when stimulated to attach the spermatheca, it appears that if several males are available, fertilization will likely occur when the female is in the right physiological state.

A few adults were exposed to daily alternated temperatures in the order of 32°-27°, 37°-32°, 37°-40°, 37°-42°, and 37°-44°C. for 5 to 7 months, unless death occurred sooner. The insects were exposed for 16 hours at the first and 8 hours at the second temperature listed in the alternation. The females exposed at 37°C. in the alternation were in environments suitable for reproduction. No evidence of a stimulating effect on oviposition was apparent.

Behavior Response to Temperature and Moisture. Twenty-five adults (numerous nymphs and adults were added from time to time) were placed for about 18 months in a heated chamber about 3 feet long having a gradient in temperature from about 60° at one end to 22°C. at the other. These specimens had been exposed previously to various temperature and moisture conditions. The relative humidity was maintained at approximately 76%. The insects tended to congregate in a region having a temperature of 35° to 42°C. Occasional excursions were made to the warm end to as high as 50°, while frequent excursions were made to the cool end of the chamber. Occasionally 2 or 3 individuals would come to rest in the cool region for some time. Eggs were deposited in food in the warm region near 38°C. After an exposure in this chamber for several weeks a secondary place of

TABLE 10. THE EFFECTS OF NUMBERS OF FEMALES OF *Thermobia* PER CAGE ON TOTAL REPRODUCTIVE RATE.

Number of ♀♀	Number of ♂♂	First reproduction after exposure. Days	NUMBER OF EGGS		AVERAGES	
			Lots	Number	Per cage	Total
1	4	18	7	81	81	
1	4	18	1	13	13	
1	4	41	5	75	75	43
1	4	18	2	25	25	
1	4	18	3	31	31	
1	4	18	2	33	33	
5	4	18	..	127	25	
5	4	18	..	277	55	
5	4	18	..	191	38	53
5	4	26	..	287	57	
5	4	8	..	236	47	
3	6	11	..	365	122	

congregation was observed. This was near one of the sources of moisture where the temperature was about 24°C., thus showing a definite reaction to moisture. Usually less than one-fourth of the total number congregated in this secondary region at any one time.

Longevity. Further evidence of the effect of the various temperature and moisture conditions is more clearly shown by considering the length of life of individuals in the various conditions. The results given in Table 11 show this very strikingly. The record of the longest living individual only is shown for each environment. Frequently other individuals lived almost as long. The captured individuals were of unknown ages when first exposed, but were mature or nearly so at that time. A humidity of 12% to 32% was very injurious and killed the insects in a few days. As one might expect the effect was lessened with a reduction in temperature. Usually a noticeable shriveling of the insects could be detected several days preceding death in temperature environments below 44°C. These shriveled individuals readily recovered when placed in moist environments, except in

advanced cases of desiccation. When placed in the vicinity of water none
of the desiccated insects responded to it, but some imbibed the liquid freely
when placed in contact with it. A humidity of 48% to 56% falls near the
border of the favorable zone (Fig. 3). Here again the greatest length of
life occurred below 40°C., but the great increase in days lived over that in
lower humidities shows that these conditions can be tolerated for long periods.
The greatest number of long-lived individuals was in humidities ranging
from 64% to 85%. Several individuals lived over 2 years, some being
of unknown age but mature when captured. Apparently temperatures of

TABLE 11. THE GREATEST LENGTH OF LIFE IN DAYS OF *Thermobia* AT VARIOUS TEMPERA-
TURES AND IN CONSTANT HUMIDITIES. THE LETTER *c* INDICATES NYMPHS REARED
FROM EGGS, ALL OTHERS WERE CAPTURED; *a* INDICATES NEXT LONGEST
LIVING INDIVIDUAL LIVED 385 DAYS; + INDICATES THAT EXPOSURE
IN THAT PARTICULAR ENVIRONMENT WAS DISCONTINUED.

Temp. °C.	LENGTH OF LIFE IN A HUMIDITY OF			
	12–32 %	48–56 %	64–85 %	97–100 %
22	30	300	418	316
27	19	682	757e	599+
29	..	....	552e	....
32	14	260	1033e	239e
37	10	675a	661	109
40	10	87	218+e	209e
42	4	253+e	239e	228
44	5	247e	359e	103e
47	2	12	18	11
52	..	.16	.16	.16

27° to 37°C. with this humidity range were far superior to other conditions
for length of life. High humidities, 97% to 100%, were unfavorable, es-
pecially at higher temperatures. Such conditions can be tolerated, however,
and reproduction occurred at times. Within the range of environments where
mature specimens could be reared from the egg (32° to 44°C. and 48% to
100%) a large majority of the long-lived individuals were reared specimens.

Extreme High Temperatures. The results from the exposure of a number
of nymphs and adults to high temperatures are given in Tables 12 and 13.
When the injury from high temperature is sufficient to incapacitate the speci-
mens so that they cannot crawl (Table 12) recovery does not occur. Tempera-
tures above 55°C. killed the insects in a few minutes, but between 48° and
55°C. signs of life were visible for some hours after they became incapaci-
tated. The length of the exposures necessary to produce death is shown in
Table 13. One individual apparently was not injured after being exposed to
52°C. for 32 hours. This was the only survivor of 65 individuals exposed to
temperatures ranging from 48° to 52°C. The maximum temperature that
could be withstood by most individuals for a few days or more is 47°C.
Sixty-seven nymphs and adults were exposed at this temperature. Fifty-one
were killed in 19 days or less, while 16 lived longer periods, one nymph sur-

viving a 47-day exposure. Heat-injured individuals appear partially paralyzed, sometimes for several days before death or after removal from extreme temperature.

Table 12. The length of life of *Thermobia* adults at extreme high temperatures. Data recorded by Harold Morland, m. s. c., 1935.

Temp. °C.	Number exposed	Time to incapacitate. Minutes
69.4	1	2
67.5	1	2
66.1	1	2
63.9	1	2
62.8	1	2
60.6	1	2
59.4	1	3
57.7	1	3
55.3	1	5
54.2	1	12
52.5	4	15.6
50.3	3	33
48.1	2	167

Table 13. The length of life of *Thermobia* at extreme high temperatures.

Temp. °C.	Number exposed	Adults or nymphs	Dead at end of	Alive after
52	51	AN	1.5–36 hours	..
52	1	N	...	32 hours
50	10	AN	2.5–14 hours	..
49	1	A	1–4 hours	..
48.5	1	A	23–28 hours	..
48	1	A	6 hours	..
47	8	AN	.25–.5 days	..
47	37	AN	.2 days	..
47	5	A	6–12 days	..
47	1	A	19 days	..
47	1	A	25 days	..
47	13	A	...	17–21 days
47	1	N	...	29 days
47	1	N	...	47 days

Fertilization. It has been observed that unfertilized females never reproduce. Frequently females reproduce in 1 to 2 weeks after being placed with the males. True copulation does not occur (see mating). The results from a number of females kept separate from males for definite periods are given in Table 14. Some of the females were kept with males for short periods of time only. One lot of 5 sisters (Nos. 1 to 5) were reared together. The ovipositors were visible on all of them when 47 days old. Two of these females were placed with males at that time. One of these laid eggs 13 days later. The other female oviposited months later after being placed with other males. Two of the sisters were placed with males 16 and 77 days after maturation, the latter to several males. Neither of these laid eggs. The fifth sister was not placed with males and died when 179 days old without opivositing. Since only the

two females that were placed with males at maturity reproduced, it suggested that fertilization near the time of maturation might be necessary. In order to test this hypothesis a new series (Nos. 1 to 19) was started. These males and females were reared from 3 lots of eggs laid on approximately the same date. The specimens were isolated when 1 month old and reared to maturity separately. The females were allowed to remain with males at different ages and for various periods of time. Nos. 6 to 10 were placed with males for periods of 1 to 4 weeks as soon as their ovipositors were visible. Nos. 11 to 19 were placed with males when approximately 1, 2, 3, and 4 months beyond the maturation stage. Successful fertilization occurred in 33% of the associations with a single male of the same age as a female. Fourteen females were placed with males a second time or from the start of the test with several

TABLE 14. THE RELATIONSHIP BETWEEN TIME OF MATING AND REPRODUCTION OF
Thermobia WHEN EXPOSED AT 37°C. AND IN 76% RELATIVE HUMIDITY.

Age when mature. Days	Days between maturation and association with males	Days With Males		Number of Eggs Laid		Days with males before ovipositing
		First time	Second time	After first males	After second males	
47	0	cont.	..	22	..	13
47	0	"	..	11	..	345
47	16	"	..	0	..	..
47	77	"	..	0	..	..
47	..	..	..	..	..	..
102	0	7	..	0	..	..
125	0	7	19	0	10	19
118	0	14	30	0	35	30
115	0	21	42	5	0	21
125	0	28	42	0	0	..
118	0	cont.	..	35	..	235
139	30	"	..	31+	..	29
137	30	"	19	7	22	8
145	60	"	..	17+	..	205
145	60	"	19	0	0	..
173	90	"	..	88	..	25
151	90	"	..	88	..	25
165	120	"	..	37	..	73
165	120	"	19	0	23	7

males of variable ages. Most of the females laid eggs. It appears that the age of the male and female is not an important factor in successful fertilization. Individuals of the same age do not necessarily succeed in fertilization. The ages of maturation of the females that reproduced were quite varied, suggesting that rate of maturation has no effect on fertilization. Two females were 145 and 118 days old and had been with males for 7 and 8 months respectively before laying eggs. It appears that fertilization can be successful at least from the time of maturation to several months after maturation and even throughout life, provided the physiological condition of both sexes is suitable.

A further test of groups of young females associated intermittently with

approximately an equal number of males is shown in Table 15. The females were reared specimens that had not reproduced when the test was started. Each cage contained 5 females at the start and the tests were continued until all had died. Males were added so as to have 3 to 5 in the cages at all times. Egg laying after separation from males occurred once, 9 days after removal. It is evident this female was fertilized before the males were removed. One egg was recovered from the same cage in another instance 22 days after males were removed. The embryo failed to develop, suggesting it was an infertile egg; probably left in the cage when the males were removed. These data clearly demonstrate that fertilization is necessary for reproduction, that fertilization must occur frequently, and that fertilization and reproduction can take place repeatedly throughout the greater part of the mature life. Occasionally females oviposited in the instar preceding death. Frequently females failed to reproduce during or following long association. Usually the

TABLE 15.   THE EFFECTS OF INTERMITTENT ASSOCIATION OF FEMALES OF *Thermobia* WITH MALES.

Number of ♀♀	Days with ♂♂	First reproduction after association. Days	Total number of eggs	Days without ♂♂	Number of eggs	Number of ♀♀ left	Days with ♂♂	First reproduction after association. Days	Total number of eggs	Days without ♂♂	Number of eggs	Number of ♀♀ left	Days with ♂♂	First reproduction after association. Days	Total number of eggs
5	51	25	52	69	0	3	53	32	34	49	0	2	Cont.	10	92
5	51	38	33	69	0	5	53	14	58	49	0	2	"	..	..
5	51	21	38	69	1	3	53	22	32	49	22	2	"	20	37+
5	50	17	115	69	0	4	53	14	60	49	0	2	"	19	42

addition of several males to a cage with females increased the number of eggs laid. Careful observation of pairs shows that the two sexes must molt within a few days of each other for successful fertilization to follow (Table 16). The results show that with 16 lots of eggs from 2 females, the males molted on or within a period of 3 days before or 5 days after the females. This suggests that the females are capable of or stimulated to attach the spermatheca only during about the first half of each instar. Fertilization must take place for each lot of eggs, and only one lot of eggs is deposited during an instar.

Ventral Abdominal Styli. It was shown in Table 4 that the ventral abdominal styli usually appeared in the fifth to tenth instars. The females typically have 3 pairs and this can be used as a partial means of determining the sexes. An occasional female may have only 2 pairs of styli. The males typically have 2 pairs, but a third pair or one stylus of the third pair frequently develops. Apparently the number of styli other than the typical, does not indicate intersexes as reproduction of such individuals was normal. A more detailed report regarding the development of the styli is being published elsewhere (Sweetman & Whittemore, 1937).

TABLE 16. THE RELATIONSHIP OF TIME OF MOLTING OF THE SEXES OF
Thermobia AND REPRODUCTION.

Instar of female	Number of eggs laid	♀ oviposited after molt. Days	♂ molted before or after ♀. Days
14	2	5	3b
16	13	4	2b
17	22	5	0
20	24	3	1a
21	19	5	3a
22	16	7	0
26	28	5	1b
27	1	9	0
29	25	5	4a
30	7	6	..
31	11	7	..
35	1	1ʋ	0
17	15	..	..
18	15	..	..
19	1	5	2a
20	12	6	..
21	14	8	4a
22	9	4	5a
23	13	5	..
24	6	..	..
29	6	8	2b
31	16	8	0
53	1	10	0

CONCLUSIONS

The firebrat is a common household pest that is a general scavenger and feeds on many carbohydrate and protein containing foods as well as starchy paper and cloth. Since it tends to remain hidden during the day, much of its damage to food remains unnoticed or is discovered only after much feeding has occurred.

The firebrat can be reared and bred continuously in cages, provided the physical environment and food are suitable. The insect requires a high temperature and relative humidity for development. The general optimum physical environment for all stages is near 37°C. and 84% relatively humidity. In such environments with ample food the firebrat has the potential to become very abundant and consequently capable of producing considerable damage to materials that the insect will eat.

Eggs. Hatching of the eggs occurs in environments ranging from 24° to 47°C. and moisture ranges of 12% to 100% humidity. The eggs can withstand considerable periods of exposure below 24°C. and still hatch if placed in favorable environments. The optimum condition for incubation of the eggs is near 37°C. and 84% humidity. Light at ordinary exposures has no effect on hatching of the eggs. The incubation period ranges from about 75 days at 24° to about 9 to 10 days at 47°C. The incubation period under optimum conditions requires 12 to 13 days.

Nymphs. The nymphs will develop to maturity in environments ranging from 27° to 44°C. and moisture ranges of 48% to 100% humidity. The optimum physical conditions for maturation of the nymphs is near 38°C. and 84% humidity. Maturation occurs in 2 to 4 months in optimum environments. The nymphs are readily killed by temperatures below 0° and above 44°C. No definite reaction to ordinary light occurs.

Adults. The adults develop eggs and oviposit at temperatures ranging from 32° to 41°C. and moisture ranging from 48% to 97% humidity. The optimum conditions for reproduction are near 37°C. and 84% humidity. The eggs are laid in crevices or hidden in food or debris. Only a few individuals can withstand temperatures above 47° C. for more than a few days. The average number of eggs per female is near 50, although wide variations in the number deposited by individual females occur. The length of life in favorable environments is about 2 to 2.5 years at 32° and about 1 to 1.5 years at 37°C. Oviposition at 37°C. occurs from about an age of 2 months to the end of life. Only 1 lot of eggs is laid during an instar and fertilization must precede each oviposition.

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